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Cover Illustration: Images from the study of *Methona curvifascia* immature stages at Garzacocha, Provincia Sucumbios Ecuador. Clockwise from top left: fifth instar, pupa, ventral adult and dorsal adult.

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COMPARATIVE STUDIES ON THE IMMATURE STAGES AND DEVELOPMENTAL BIOLOGY OF FIVE *ARGYNNIS SPP.* (SUBGENUS *SPEYERIA*) (NYMPHALIDAE) FROM WASHINGTON

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ABSTRACT. Comparative illustrations and notes on morphology and biology are provided on the immature stages of five *Argynnis spp.* (*A. eybele leto, A. coronis simaetha, A. zerene picta, A. egleis medunnoughi, A. hydaspe rhodope*) found in the Pacific Northwest. High quality images allowed separation of the five species in most of their immature stages. Sixth instars of all species possessed a fleshy, eversible osmeterium-like gland located ventrally between the head and first thoracic segment. Dormant first instar larvae of all species exposed to summer-like conditions (25 ± 0.5° C and continuous illumination), 2.0–2.5 months after hatching, did not feed and died within 6–9 days, indicating the larvae were in diapause. Overwintering of first instars for ~ 80 days in darkness at 5 ± 0.5° C, 75 ± 5% r.h. resulted in minimal mortality. Subsequent exposure to summer-like conditions (25 ± 0.5° C and continuous illumination) resulted in breaking of dormancy and commencement of feeding in all species within 2–5 days. Durations of individual instars and complete post-larval feeding development durations were similar for *A. coronis, A. zerene, A. egleis* and *A. eybele* (54.1–55.5 days from post-diapause first instars to adulthood). Development of *A. hydaspe* was significantly faster averaging 47 days. Larvae of all species readily accepted *Viola adunea* and *V. glabella* as host plants. *Viola labradoriea* was also accepted by all instars of *A. egleis*, however, its acceptance was limited in the other species to later instars. Domesticated pansies (*Viola tricolor*) were accepted by sixth instars of *A. egleis, A. coronis* and *A. zerene*, but only limited feeding occurred with sixth instar *A. eybele*.

Additional key words: morphology, osmeterium, development, diapause, host plants, overwintering, instar durations

Nine species of Greater Fritillary (*Argynnis spp.*) occur in Washington: *A. cybele* (F.), *A. coronis* (Behr), *A. zerene* (Boisduval), *A. callippe* (Boisduval), *A. egleis* (Behr), *A. hesperis* (Edwards), *A. atlantis* (Edwards), *A. hydaspe* (Boisduval) and *A. mormonia* (Boisduval) (Guppy and Shepard 2001, Pyle 2002, Warren 2005). Until recently, these species, along with all North American Greater Fritillaries were considered to belong to the genus *Speyeria*. However, recent morphological and molecular studies by Simonsen (2006) and Simonsen *et al.* (2006) showed that the North American species are better treated as members of the large, unified genus, *Argynnis* with *Speyeria* relegated to a sub-genus. The immature stages of *Speycria* spp. are generally infrequently encountered and are thus poorly described or illustrated. Detailed morphological studies and descriptions of *Argynnis* eggs, larvae and pupae may yield important distinguishing characteristics that could be useful along with adult characteristics for resolving taxonomic issues with the many subspecies and putative subspecies that occur in this genus (Warren 2005). Similarly, the biology of immature *Argynnis* spp. is also imperfectly known and offers a field rich in potential for understanding mechanisms of diapause, defense, host plant relationships etc.

This paper provides biological information on, and detailed illustrations of the immature stages of five Washington *Argynnis* spp., *A. cybele* leto (Behr), *A. coronis* simaetha dos Passos and Grey, *A. zerene* picta (McDunnough) , *A. egleis* medunnoughi (Gunder) and *A. hydaspe* rhodope (W. H. Edwards). Of the five, only the endangered Oregon coast subspecies of *A. zerene* (*A. z. hippolyta* (W. H. Edwards)) has received detailed attention to its immature stages within the past 25 years (McCorkle 1980, McCorkle and Hammond 1988). The early stages of eastern North American *A. cybele* and *A. egleis* from Nevada were described more than 125 years ago by W. H. Edwards (Edwards 1879, 1880). Descriptions and illustrations of late instars only, are available for *A. eybele, A. coronis, A. zerene* and *A. hydaspe* (Comstock and Dammers 1931, Dornfeld 1980, Scott 1986, Allen 1997, Guppy and Shepard 2001, Miller and Hammond 2003, Allen *et al.* 2005, Wagner 2005). Allen *et al.* (2005) described the late instar larva

of *A. egleis* but did not illustrate it. Aside from *A. z. hippolyta*, very little has been reported on the biology and ecology of the immature stages of these five species (Pyle 2002, Warren 2005).

During August 2005 to April 2006, *A. cybele*, *A. coronis*, *A. zerene*, *A. egleis* and *A. hydaspe* were reared in the laboratory, for photography of all the immature stages (including each instar). Notes on coloration, patterning and dimensions of eggs, larvae and pupae were made. Observations were also made on aspects of biology such as overwintering mortality, diapause, host plant acceptance and developmental duration.

MATERIALS AND METHODS

Gravid females of *A. cybele leto* (2), *A. coronis simaetha* (4), *A. zerene picta* (10), *A. egleis mcdunnoughi* (4) and *A. hydaspe rhodope* (4), were obtained during August 2005 from the Umatilla National Forest in SE Washington (*A. c. leto*, *A. z. picta*, *A. e. mcdunnoughi*) and Wenatchee National Forest on the eastern edge of the Cascade mountains (*A. c. simaetha*, *A. h. rhodope*). Females were placed in plastic buckets (31 cm deep, 28 cm diameter) with muslin-covered lids and held at 21–28° C under natural daylength. Butterflies were provided with potted violets (*Viola labradorica* Schrank) or dessicating violet foliage (*Viola adunca* Sm., *V. labradorica*, *Viola glabella* Nutt.) and paper toweling as oviposition substrates and tissue pads soaked in sugar/water solution for nourishment. Butterflies oviposited freely under these conditions. Eggs were measured, photographed and left in the buckets to hatch. First instars were also measured and photographed and along with all violet foliage and paper toweling, were transferred to plastic boxes (30 × 23 × 10 cm) with muslin lids. The boxes were held at 20–28° C under natural daylength until September 3 when they were transferred to shaded outdoor conditions until October 31 (10–25° C). During this period, larvae were exposed to fine water-misting every 2–3 weeks.

Larval diapause termination experiment. On October 31, five first instars of *A. coronis*, *A. zerene*, *S. cybele* and *S. hydaspe* were transferred to summer-like (25 ± 0.5° C, constant fluorescent illumination) conditions and placed on fresh, detached *V. adunca* leaves laid upperside down on wet cotton wool in a muslin-covered plastic Petri-dish (13 cm diameter). Observations on behavior and mortality were made daily.

On November 1, plastic boxes containing remaining dormant larvae were transferred to a dark constant temperature room set at 5 ± 0.5 C for overwintering. Relative humidity was maintained at 75 ± 5 %. Overwintering larvae were transferred to summer-like conditions (25 ± 1° C, constant fluorescent illumination) during 11–19 January. One group of 12 *A. coronis* larvae was transferred on January 4 to 15–21 ° C/ 9 hrs light. First and second instars were reared on detached *Viola* leaves placed upper surface down on moist cotton wool in muslin-covered plastic Petri dishes (13 cm diameter). Dried leaf debris was provided as shelter for the larvae. Third-sixth instars were reared in plastic boxes (25 × 15 × 6 cm) with muslin lids. Cut *Viola* spp. with stems in water was provided for food and shelter. Pre-pupal sixth instars were placed in larger boxes (30 × 23 × 10 cm) with a greater amount of foliage to provide pupation sites. All instars and pupae were photographed. Observations on larval morphology, coloration, behavior, development, host plant acceptance and mortality were made daily until pupation.

Photographs were taken using a Canon EOS 1DS Mark II, digital SLR camera mounted on a tripod. A Canon MP-E 65 mm 1 X – 5 X macro lens was used together with a Macro Twin Lite MT – 24 EX flash lighting system.

RESULTS

Morphology of immature stages. Eggs, instars 1–6 and pupae of *A. coronis simaetha*, *A. zerene picta*, *S. egleis mcdunnoughi*, *A. cybele leto* and *A. hydaspe rhodope* are shown in Figs. 1–2. Eggs of all species were creamy white when freshly laid, turning orange or pinkish/tan/brown with development after 2–3 days. Egg dimensions were comparable between species, being 0.9–1.0 mm in height and 0.8–1.0 mm in diameter (Table 1). The eggs of *A. zerene* were generally the smallest (0.9 × 0.8 mm) and were noticeably more ovoid than eggs of the other species. Eggs of *S. egleis* and *S. cybele* were flattened basally, while the eggs of *S. coronis* and *S. hydaspe* were more cylindrical (Figure 1).

First instars of all species measured approximately1.5 mm after hatching but increased to 1.75–2.0 mm after imbibing water droplets. Lengths of larvae at the beginning and end of each instar for the five species are shown in Table 1. Generally, there was good correlation of instar sizes between species with an approximate doubling of size with each instar from one to three, a lessening of growth rate in instars 4 and 5, then an increase in the sixth instar. Mature larvae of *A. cybele* were largest at 45 mm with the other four species similarly sized, ca. 35–38 mm (Table 1). Coloration of unfed first instars varied with *S. coronis* and *S. hydaspe* generally lighter colored than the other three species (Figure 1). All species had black head capsules. In general the black tubercles running longitudinally down the body were darker and more prominent in first

instars of *S. egleis* and *S. eybele* than the other three species. Fine dark hairs arose from these tubercles and appeared in all species to secrete a small droplet of fluid at the distal end. Second instars were characterized by the development of spines, replacing the hairs rising from the tubercles. Head capsules were black and the five species were generally similarly-colored in this instar. A light colored dorsal band was evident in *A. eybele* and all species had a lower lateral row of orange/tan-colored tubercles. Third instars showed greater spinc development, particularly in *A. hydaspe* (Fig.1) and the lower lateral row of orange tubercles was more prominent in all species. In addition, the upper lateral row of tubercles was also orange in this instar. This was particularly pronounced in *A. coronis* and *A. zerene*. Head capsules remained solid black except for *A. hydaspe* which showed limited orange/brown marking. All species except *A. hydaspe* had a prominent pale dorsal band in the third instar with a central darker colored intermittent stripe running through the center. The lower lateral row of orange tubercles was further developed in the fourth instar of all species. The upper lateral row was also strongly developed in *A. eybele*, *A. coronis* and *A. zerene* but virtually lacking in *A. hydaspe* and *A. egleis*. The pale dorsal band with intermittent central dark stripe was also further developed in fourth instar *A. coronis*, *A. zerene* and *A. egleis*, but absent in fourth instar *A. eybele* and *A. hydaspe*. Ground color of fourth instar *A. coronis*, *A. zerene* and *A. egleis* was gray/white rather than black as in *A. eybele* and *A. hydaspe* (Fig. 1). Head capsules of fourth instars were largely black with varying amounts of orange-brown on dorsal surfaces, most pronounced in *A. eybele* and *A. hydaspe* and least in *A. coronis*. Fifth instars were very similar to fourth instars in coloration, although *A. coronis* tended to be a little darker in this instar. The orange-brown dorsal markings on the head capsule were more pronounced in *A. eybele*, *A. hydaspe* and *A. egleis* in the fifth instar. Lateral and dorsal views of sixth instar larvae are shown in Fig. 2. The upper lateral row of orange tubercles was most developed in *A. eybele* and *A. egleis*, although they tended paler, almost white, in the latter species. In *A. zerene* the color of these tubercles was brown or black and blended in with background coloration (Fig. 2). The same was true for *A. coronis* except on the first two abdominal segments where the upper row of tubercles remained orange. The upper lateral tubercles on the first two abdominal segments of *A. egleis* sixth instars were also more vividly colored than the rest of this row. Dorsal coloration of *A. zerene* and *A. coronis* was palest contrasting with the black ground color of *A. eybele* and *A. hydaspe*. The dorsal ground color of *A. egleis* was intermediate lacking the distinctive gray/tan/white blotches of *A. zerene* and *A. coronis* (Fig. 2). The pale dorsal band containing an intermittent central dark stripe was still present in *A. coronis* and *A. zerene* but absent in the other species. Dorsal orange-brown coloration of the head capsule extending laterally was most developed in *A. eybele* and *A. egleis*, with only very minor orange coloration on the

TABLE 1. Sizes (mm) of immature stages of five *Argynnis* spp. Egg dimensions are height × width. Larval dimensions are lengths measured at commencement and end of each instar. Egg and larval data were obtained from examination of 2–4 individuals. Variation was generally less than 0.1 mm. Pupae were measured from cremaster to tip of head (Mean ± SE) (number of pupae examined in parentheses).

	S. coronis simactha	***S. zerene picta***	***S. egleis mcdunnoughi***	***S. cybele leto***	***S. hydaspe rhodope***
Egg	1.0 × 0.9	0.9 × 0.8	1.0 × 1.0	0.9 × 0.9	1.0 × 0.8
First instar	1.5 – 3.0	1.5 – 2.5	1.5 – 3.0	1.5 – 3.0	1.5 – 3.0
Second instar	3.0 – 6.0	2.5 – 4.0	3.0 – 5.0	3.0 – 5.0	3.0 – 6.0
Third instar	6.0 – 10	4.0 – 8.0	5.0 – 8.0	5.0 – 9.0	6.0 – 10
Fourth instar	10 – 15	8.0 – 13	8.0 – 13	9.0 – 15	10 – 15
Fifth instar	15 – 20	13 – 20	13 – 20	15 – 25	15 – 19
Sixth instar	20 – 35	20 – 38	20 – 35	25 – 45	19 – 37
Pupa	23.5 ± 0.2 (4)	23.6 ± 0.6 (10)	22.7 ± 0.2 (7)	28.5 ± 0.2 (4)	22.0 ± 0.9 (4)

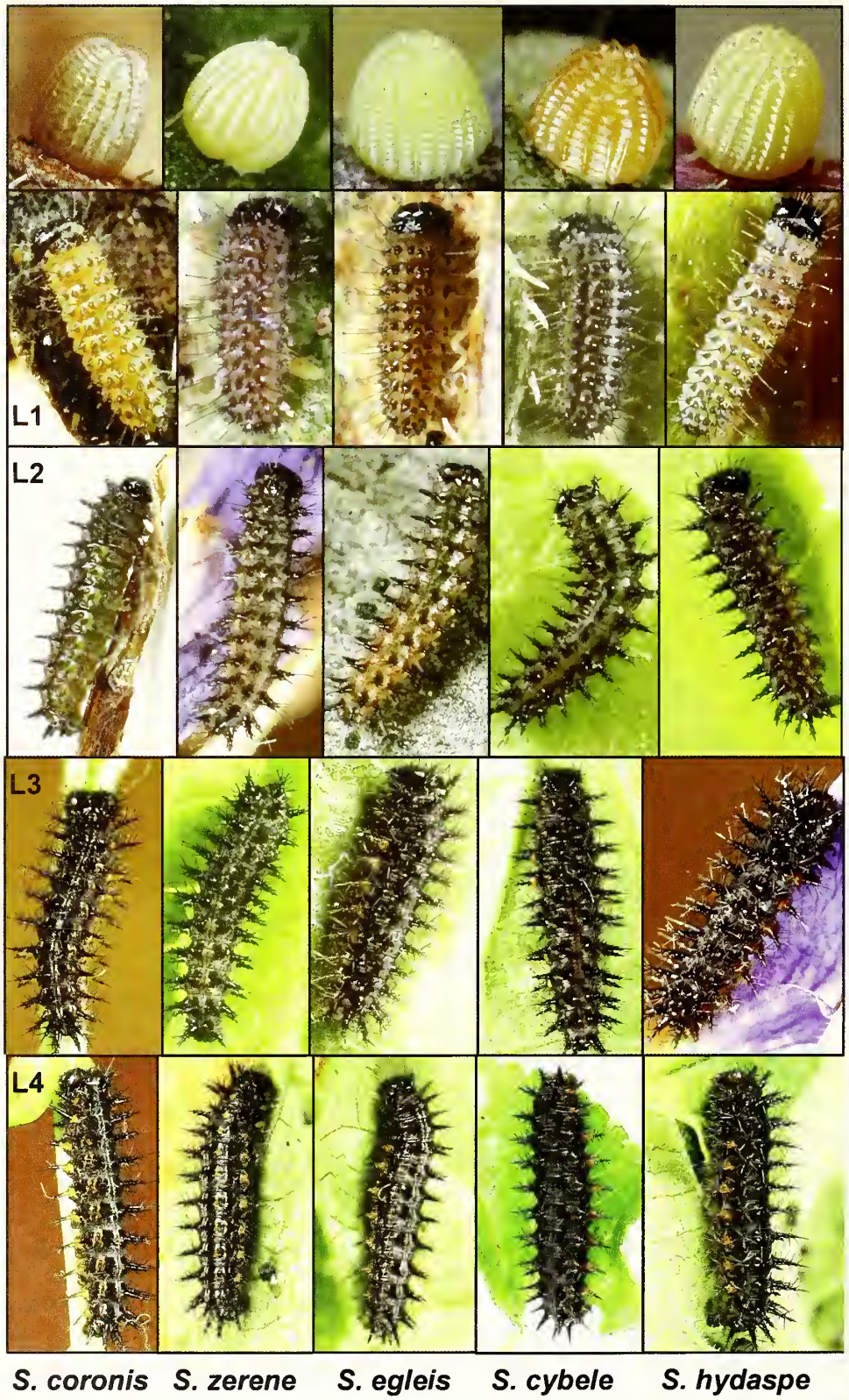

FIG. 1. Eggs and first four instars of *A. coronis simaetha*, *A. zerene picta*, *A. egleis mcdunnoughi*, *A. cybele leto* and *A. hydaspe rhodope*.

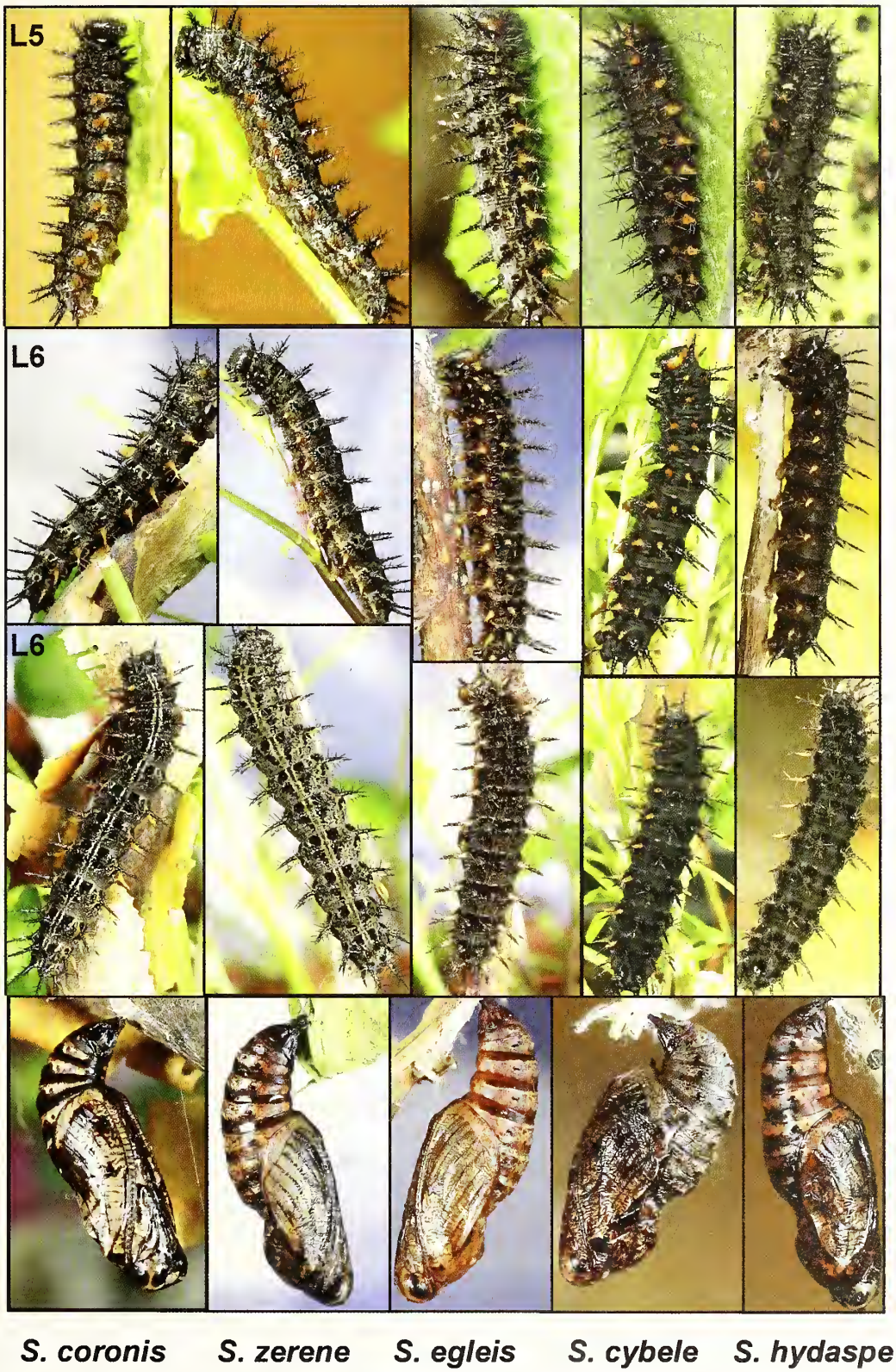

FIG. 2. Fifth and sixth (ventral and dorsal views) instars and pupae of *A. coronis simaetha*, *A. zerene picta*, *A. egleis mcdunnoughi*, *A. cybele leto* and *A. hydaspe rhodope*.

head capsules of *A. zerene* and *A. hydaspe*. No orange coloration was seen on the all black head capsules of sixth instar *A. coronis*.

Sixth instars of all species possessed a fleshy, eversible osmeterium located ventrally between the head and first thoracic segment (Fig. 3). A musky odor emanating from the organ was apparent when the larvae were handled roughly. Further examination of *A. egleis* larvae showed that the organ was not present in first instars but appeared in the second instar and was present in all subsequent instars.

Sixth instars were mature at maximum recorded lengths of 35 (*A. egleis*, *A. coronis*), 37 (*A. hydaspe*), 38 (*A. zerene*) or 45 mm (*A. cybele*) (Table 1). The pupa of each species is illustrated in Fig. 2 and lengths are shown in Table 1. The pupae of *A. coronis* and *A. zerene* were most similarly colored (shades of brown with variable black markings) although *A. coronis* pupae tended to be more darkly pigmented with more prominent black banding on the anterior edge of each abdominal segment. Wing venation in *A. zerene* pupae was generally highlighted in black (Fig. 2). The pupa of *A. egleis* was light brown with the least dark pigmentation of the five species. The pupa of *A. hydaspe* was similar to those of *A. coronis* and *A. zerene* although was generally more darkly pigmented. The pupa of *A. cybele* differed from the others by having a rougher texture and greater girth, as well as having greater length. It was similarly colored to the pupa of *A. hydaspe*.

Oviposition, egg and pre-diapause biology. Oviposition by females of the five species occurred between 2 and 8 days after caging, resulting in ~50 eggs each for *A. egleis*, *A. coronis* and *A. cybele*. Approximately 30 eggs were obtained from *A. hydaspe* females and an estimated 250 from *A. zerene* females. Females of *A. hydaspe* and *A. egleis* took 2 days to oviposit after capture on August 1 and 3, respectively. Females of *A. zerene* took 6 days after capture on August 3 and *A. coronis* females oviposited 7 days after capture on July 30th. Females of *A. cybele* oviposited 8 days after capture on August 20. All females generally oviposited on dessicated *Viola* leaves and stems, paper toweling, and muslin lids. However, *A. hydaspe* and *A. egleis* initially (first 48 h of oviposition) only oviposited on potted *V. labradorica*, ignoring dessicated foliage. In contrast, *A. coronis* oviposited only on dessicated leaves and stems despite the presence of potted *V. labradorica*. Eggs of the five species took between 9 and 14 days to hatch under temperatures that fluctuated between 20–28° C (Table 2). First instars did not wander far from their egg shells but sought out refugia such as curled leaves before becoming quiescent. Examination of the larval cultures of all species on October 31 indicated substantial mortality of *A. zerene* larvae had occurred, leaving only an estimated 50 (from 250) larvae still alive. In contrast, very little (< 5 %) mortality was evident in the cultures of the other species.

Larval diapause termination experiment. All dormant first instars exposed to summer-like conditions ~ 2.0–2.5 months after hatching, died within 6–9 days. All except one *A. cybele* larva remained quiescent during this period showing no sign of feeding. The single *A. cybele* larvae wandered a little but did not feed.

Post-diapause biology. Examination of the larval cultures in early-mid January indicated good survival (>90%) of all species under 5° C conditions. Exposure of the larvae to summer-like conditions resulted in breaking of dormancy (using commencement of feeding as the criterion) in all species within 2–5 days (Table 2). Developmental durations and overall mortalities for

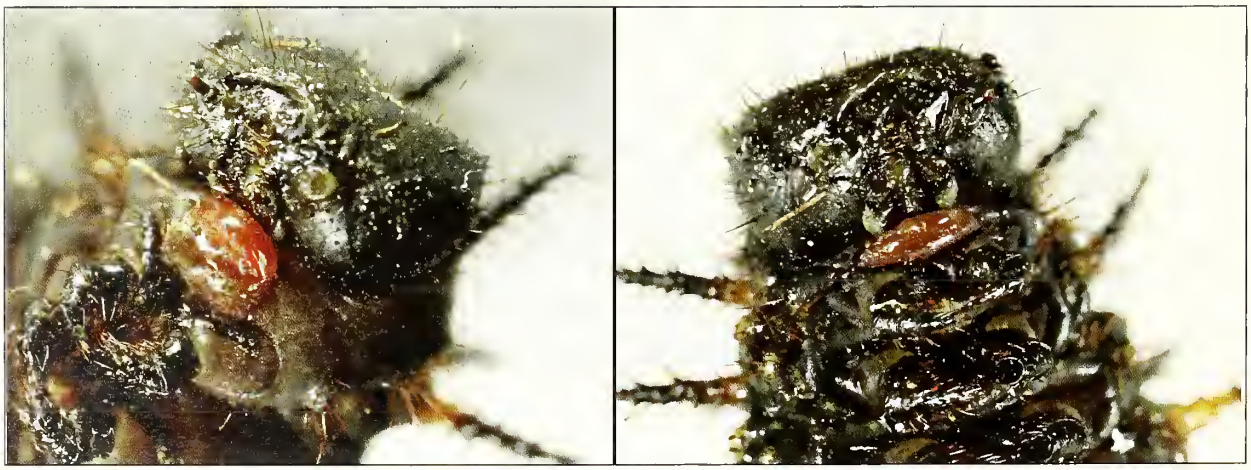

FIG. 3. Ventral gland of sixth instar *A. coronis simaetha*.

TABLE 2. Developmental durations (days) for eggs, larvae and pupae of five *Argynnis* spp. reared at 20-28° C (eggs) or 25 ± 0.5° C under continuous illumination (larvae and pupae). Pre-feeding durations represent the time between introduction of diapausing larvae into summer-like conditions and commencement of feeding. Instar duration data were obtained from first appearance of each instar among species cohorts. First-adult durations were calculated from introduction of first instars to summer-like conditions to adult eclosion (Mean ± SE) (number of individuals completing development in parentheses). *Indicates significant difference from

	A. coronis simaetha	***A. zerene picta***	***A. egleis mcdunnoughi***	***A. cybele leto***	***A. hydaspe rhodope***
Egg	14	13	14	12	9
Pre-feeding period 25°C	3	5	2	4	3
First instar	9	9	8	9	9
Second instar	7	5	5	6	8
Third instar	8	6	5	6	3
Fourth instar	4	6	5	8	3
Fifth instar	4	6	6	5	3
Sixth instar	8	11	13	10	9
Pupa	12	13	12	13	12
First - Adult	54.2 ± 0.7 (4)	55.0 ± 0.3 (10)	54.1 ± 0.2 (7)	55.5 ± 1.0 (4)	47.0 ± 1.0* (4)
% Survival First-Adult	50	50	50	50	75

larvae during post-diapause development at 25 ± 0.5° C/ 24 h light are shown in Table 2. Due to limitations in host plant availability, starting cohort sizes for each species were necessarily small (4–30 larvae). Additional larval cohorts of *A. egleis* (3) and *A. zerene* (10) exposed to these conditions from January 11 instead of January 19, were slower to start feeding and took three weeks to reach the second instar instead of just over a week for the later group. An extra group of 12 *A. coronis* larvae exposed to 15–21 °C and short days (9 h) from January 4–19 failed to break dormancy and did not feed. Durations of individual instars and complete post-larval feeding development were similar for *A. coronis*, *A. zerene*, *A. egleis* and *A. eybele* (Table 2). From their introduction to 25 ± 0.5° C and continuous illumination on January 19, these four species averaged 54.1–55.5 days to reach adulthood. In contrast, development of *A. hydaspe* was significantly faster than the other four species under the same conditions, averaging 47 days ($P < 0.05$, Mann-Whitney Rank Sum Test) (Table 2). Fifty per cent survival was obtained for all species cohorts except *A. hydaspe* in which 3 of the 4 larvae reached adulthood (Table 2).

Larvae of all species readily accepted *V. adunea* and *V. glabella* as host plants. *Viola labradoriea* was also accepted by all instars of *A. egleis*. However, its acceptance was limited in the other species to later instars (5 and 6). First instars of *A. coronis* and *A. zerene* would not feed on *V. labradoriea*. Later instars of these two species fed preferentially on *V. adunca* when supplied in combination with *V. labradoriea*. The sagebrush violet, *V. trinervata* Howell, was provided to *A. egleis* third instars only and was not accepted as a host. Domesticated pansies (*Viola tricolor* L.) were accepted by sixth instars of *A. egleis*, *A. coronis* and *A. zerene*. Only limited feeding on pansy occurred with sixth instar *A. eybele*, and *A. hydaspe* was not evaluated.

Mature larvae of all five species constructed 'leaf tents' from strategically silked leaves for pupation, in which they spun a silk pad for cremaster attachment. This behavior was strongly entrenched, taking place even when insufficient space within the 'tent' was available for 'hanging'. The silken pads or cremaster attachments were insufficient in many cases with pre-pupae or pupae falling to the ground. Pupal development durations are provided in Table 2. The pupae of *A. eybele* were noticeably more active (wriggling at slightest provocation) than the pupae of the other species. Relative humidity of ~ 40% at 25 ± 0.5° C caused desiccation of many pupae. Noticeable protandry occurred only with *A. zerene* and *A. eybele*; males of these species emerged ~ 4–5 days earlier than females.

DISCUSSION

Comparative illustrations and notes on the morphology and biology of immature stages of five *Argynnis* spp. commonly found in the Pacific Northwest

are provided for the first time. High quality images allowed separation of the five species in most of their immature stages. Prior to this study, only the endangered, coastal *A. zerene hippolyta* had received detailed attention to its immature stages including aspects of biology (McCorkle 1980, McCorkle and Hammond 1988). Aside from some very old descriptions of the early stages of *A. cybele* and *A. egleis* (Edwards 1879, 1880), only descriptions/illustrations of late instars were available previously for the five species covered here (Comstock and Dammers 1931, Dornfeld 1980, Scott 1986, Allen 1997, Guppy and Shepard 2001, Miller and Hammond 2003, Allen *et al.* 2005, Wagner 2005).

Oviposition was obtained readily within a few days by females of *A. coronis*, *A. zerene*, *A. egleis* and *A. hydaspe* collected in late July or early August. Most *Argynnis* spp, including those in this study, are thought to undergo an adult reproductive diapause for 3–5 weeks after eclosion (Sims 1984). This study indicates reproductive diapause in *A. coronis*, *A. zerene*, *A. egleis* and *A. hydaspe* terminates by early August in Washington populations. The eggs of *Argynnis* spp. do not appear to have been depicted in publications previously, except as line drawings (e.g. Scott and Mattoon 1982). Despite their obvious similarity, some subtle differences in shape appeared to be consistent between species, especially the basal flattening of *A. cybele* and *A. egleis* eggs. Edwards (1880) also noted the broad base of *A. cybele* eggs. Coloration also appeared to differ between species both in newly laid and developing eggs, but more study is needed to characterize this. Similarly, very little attention has been paid previously to first instar *Argynnis* with this study indicating at least some differences in coloration occur between species. Ground color of first instar *A. zerene*, *A. egleis* and *A. cybele* ranged between brown-purple/black while *A. coronis* and *A. hydaspe* larvae were generally cream-yellow. In all species, the unbranched setae or hairs of first instars usually carried a droplet of fluid at the distal end as is characteristic of pierid larvae (Allen *et al.* 2005). In *Pieris rapae* L. these droplets contain defensive chemicals (Smedley *et al.* 2002) and it is possible that the droplets on *Argynnis* first instars also have a defensive function. Second instars were the least species-differentiated stage, but clear differences in markings and coloration began to appear in third instars and continued until larval maturity. These differences allow good separation of species based on head capsule and body ground color, presence or absence of dorsal bands and the extent of lateral tubercle coloration. Generally, previously published descriptions/illustrations of the five late instar *Argynnis*, matched the current observations. Earlier descriptions tended to describe tubercle coloration as 'yellowish', whereas in this study, the color was clearly more orange than yellow in most cases.

The existence of a ventral osmeterium-type organ in *Argynnis* larvae, analogous to the well-known eversible dorsal defense organ of papilionid larvae (Honda and Hayashi 1995), was first observed by McCorkle and Hammond (1988) in *A. zerene hippolyta* and was also reported by Scott (1986). This study is the first to illustrate the organ. This gland, likely to be defensive in function, probably occurs in larvae of all *Argynnis* spp. Similar ventral glands were also observed in late instars of *Nymphalis vaualbum* (Denis & Schiffermuller), *Nymphalis antiopa* (L.) and *Boloria selene* (Denis & Schiffermuller) (James, unpublished observation). Scott (1986) reports occurrence of ventral glands in other nymphalid genera including *Historis*, *Smyrna* and *Anartia* and suggests they also occur in "some Pieridae, Danainae, Libytheidae, skippers and probably others" (page 71, Scott 1986). The chemical ecology of ventral glands in Washington *Argynnis* spp. is currently being researched (James, in prep).

All *Argynnis* spp. overwinter as unfed first instars which are presumed to be in diapause (Mattoon *et al.* 1971). Diapause is a physiologically defined and controlled mechanism ensuring resumption of development does not occur prematurely (Danks 1987). First instar *Argynnis* presented with normally favorable conditions of temperature during late summer and autumn do not commence feeding and development. Daylengths are declining during this time and host plants are of poor quality or unavailable and it may be these factors that directly prevent development. Exposure of first instar *A. zerene*, *A. coronis*, *A. cybele* and *A. hydaspe* in this study to summer-like conditions of temperature, photoperiod and host plant availability in late Fall, did not succeed in 'breaking' diapause in any species. This is the first experimental evidence confirming the existence of physiological diapause in first instar *Argynnis*, rather than a more flexible dormancy state (or 'quiescence' as suggested by Mattoon *et al.* (1971)) cued by declining daylength and/or host plant inadequacy. *Argynnis* spp. are among the few lepidopteran genera that have been documented to possess diapause in two life stages, larvae and adults (Sims 1984, James 1999). Approximately 80 days of exposure to a constant (5 ± 0.5°C) cool temperature and darkness, resulted in the termination of diapause within a few days in all five species when subsequently exposed to summer-like conditions. Interestingly, exposure to these conditions a week earlier resulted in much slower breaking of

diapause in *A. coronis*, suggesting that diapause development at this time was less complete. Survival of diapausing first instars confined in plastic boxes amongst leaf debris at 5 ± 0.5°C and 75 ± 5 % r.h. for ~ 80 days was high. However significant mortality (> 50%) occurred with *S. coronis*, *S. zerene* and *S. cybele* larvae held for 135 days under these conditions. In contrast, *S. egleis* larvae still showed little mortality after 135 days. This overwintering technique was a lot simpler than the small hollow wooden block technique reported by Mattoon *et al.* (1971). In the latter procedure blocks are soaked weekly to maintain high relative humidity. The key to good overwintering survival of first instar *Argynnis* appears to be adequate moisture/humidity levels but requirements may differ between species. Dry ambient conditions during September–October may have caused the substantial mortality observed among *A. zerene* larvae, although the other species were not adversely affected.

Post-diapause development rates of immature *A. coronis*, *A. zerene*, *A. egleis* and *A. cybele*, were very similar with each species taking about 54–55 days or 7.7–7.8 weeks to reach adulthood at 25° C. Although only three *A. hydaspe* larvae completed development, their mean duration of 47 days or 6.7 weeks from post-diapause first instar to adult was significantly less than for the other four species. These developmental durations are similar to what has been reported previously for *Argynnis* spp. For example, McCorkle and Hammond (1988) reported 'most subspecies of *A. coronis* and *A. zerene* required six to seven weeks for males and seven to eight weeks for females', when reared at 21–23° C. They also noted that *A. cybele* required a similar period of time. These authors did not mention *A. hydaspe*, but the duration recorded here for this species compares to the fastest rates reported in their paper for certain forms of *A. atlantis*, *A. egleis* and *A. callippe*.

Although no systematic host acceptance or preference studies were conducted, it is likely as reported previously (Mattoon *et al.* 1971), that *Argynnis* spp. differ in their acceptance of different *Viola* spp. All five species readily accepted the two Pacific Northwest endemic *Viola* spp., *adunca* and *glabella* provided to them. *Viola adunca* is recorded as a natural host for four of the five species, with *A. coronis* as the exception. *Viola glabella* is recorded as a natural host for *A. hydaspe*, *A. cybele* and *A. zerene* but not for *A. egleis* and *A. coronis* (Hammond 1983, Scott 1986, Pyle 2002, Warren 2005).

In Washington, *A. coronis* is reported to feed mostly on *V. trinervata* (Pyle 2002, Warren 2005) but *V. adunca* and *V. glabella* also occur in many *A. coronis*-occupied habitats particularly on the eastern slopes of the Cascade mountains. This study suggests the larvae of this species would have no problem utilizing this host if they encounter it. *Viola trinervata* was not accepted by *A. egleis* as a host in this study and is unlikely to grow in habitats occupied by *A. egleis*. *Viola glabella* occurs in the Blue Mountain habitat from which females were collected for this study and could be utilized as a host, given its acceptability as a larval host recorded here. *Viola labradorica* is native to the north eastern USA, and varied considerably in its acceptability to Washington *Argynnis*. First instar *A. coronis* and *A. zerene* would not feed on it and later instars of these species and *A. cybele* and *A. hydaspe* only accepted it when given no choice. In contrast, *A. egleis* accepted this host readily in all instars. Late in rearing it became necessary to supplement the diets of four species with pansies (*V. tricolor*). *Argynnis egleis*, *A. coronis* and *A. zerene* accepted this host readily, but *A. cybele* did not.

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HAWKMOTH FAUNA OF A NORTHERN ATLANTIC RAIN FOREST REMNANT (SPHINGIDAE)

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ABSTRACT. We present results of a year-long faunistic survey of Sphingidae of the Brazilian northern Atlantie rain forest. The study was undertaken between August 2003 and July 2004, at the Private Nature Reserve (RPPN) Frei Caneea in the state of Pernambuco. Hawkmoths were eaptured using a 250-watt mercury-vapor light trap positioned against a white wall. We recorded 379 individuals of 50 species in 19 genera. The most abundant speeies were *Erinnyis ello*, *E. alope*, *Neogene dynaeus* and *Protambulyx astygonus*, which accounted for 44.2% of the collected individuals. More than one individual was recorded for all but eight speeies. Hawkmoths abundanee was lowest in the months with intense rainfall. The sphingid fauna of northeastern Brazil is eompared with that of the Amazonian and southern Atlantic rain forest as well as with the adjacent caatinga, a tropieal dry forest with abundant succulent plants. Species composition of Sphingidae of the northern Atlantie rain forest was most similar to that of the Amazonian forest.

Additional key words: biodiversity, biogeography, Brazil, distribution, Pernambuco, South Ameriea, survey

The Sphingidae (Bombycoidea) includes about 1200 species globally (Lemaire & Minet 1999) and 180 species in Brazil (Brown 1986). Sphingidae are cosmopolitan and show highest diversity in the tropics (Hodges 1971). In South America, surveys of Sphingidae are scarce and regional inventories are necessary to know their diversity and distribution and to elucidate their biogeographical relationships (Kitching & Cadiou 2000).

The Brazilian Atlantic rain forest, which extends along the Atlantic coast between the states of Rio Grande do Norte and Rio Grande do Sul (Rizzini 1997), is currently highly fragmented, with only 5% of its original forest remaining (Ranta *et al.* 1998, Tabarelli *et al.* 2002). The first local survey of Sphingidae in the northern part of the Atlantic rain forest revealed 23 species (Duarte & Schlindwein 2005a). In an area of *cerrado*-like savannah vegetation of the *Tabuleiro* (tropical grassland with evergreen trees and shrubs), in the northeast Brazilian state of Paraíba, Darrault & Schlindwein (2002) recorded 24 species of sphingids. In the caatinga, the hawkmoth fauna is poor, and only 14 species were recorded in an area of caatinga in Paraíba (Gusmão & Creão-Duarte 2004) and 20 in Rio Grande do Norte (Duarte & Schlindwein 2005b). This contrasts to the high diversity of Sphingidae in the Amazon basin (Motta *et al.* 1998).

The northern Atlantic rain forest is strongly influenced by the Amazonian biota (Prance 1982, Santos *et al.* 2007). The montane forests of northeast Brazil on the other hand form a refuge for several species of plants and animals, which, due to their cooler and more humid climate, differ from the arid caatinga that surrounds them (Andrade-Lima 1982). Several botanical studies in northeastern Brazil have revealed floristic disjunctions between the Amazonian forest and the north Atlantic rain forest (Andrade-Lima 1982). This is also true for many animal taxa (Bigarella *et al.* 1975, Coimbra-Filho & Câmara 1996).

In this study we determine species richness, abundance, and seasonality of Sphingidae of a preserved area of the Atlantic rain forest in Pernambuco, northeastern Brazil, and compare the sphingid fauna to that of the caatinga and Amazonian rain forest.

MATERIALS AND METHODS

Study area. The study was carried out in the Reserva Particular do Patrimônio Natural RPPN Frei Caneca (Private Nature Reserve Frei Caneca) in the municipality of Jaqueira, Pernambuco, NE-Brazil. The study site is located at 8°42'41"S and 35°50'30"W at an altitude of 500–750 m (Fig. 1). The reserve covers an area of 630.42 ha, with a mountainous relief and granite rocky outcrops. The climate is tropical, hot and humid, with a mean annual temperature of 22°C. There is a 4–5 month dry (less-humid) season between October and February and a rainy season between March and September (IBGE 1985). The mean annual rainfall,

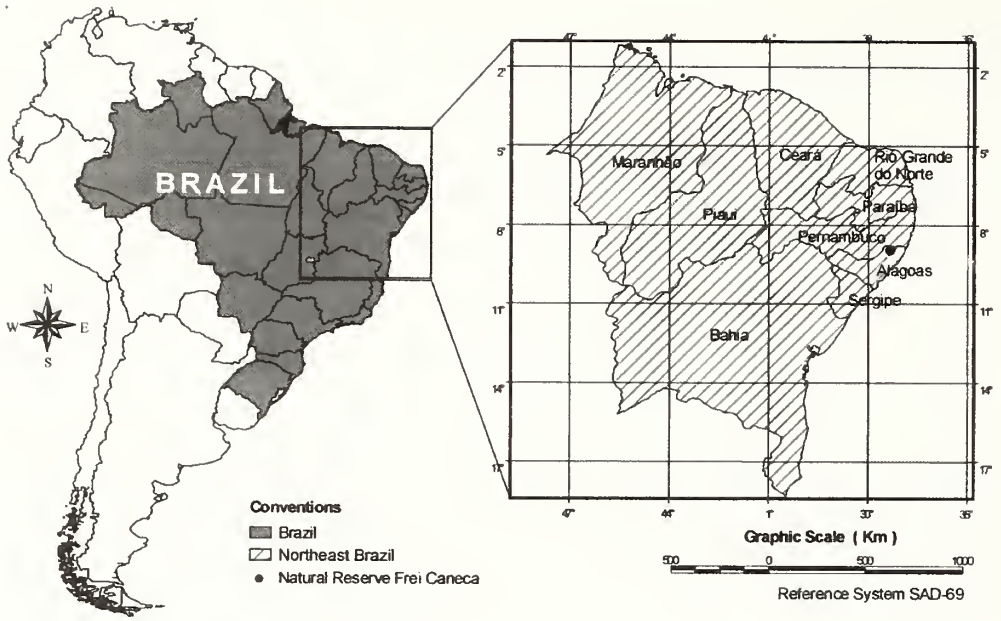

FIG. 1. Geographical location of the study site RPPN Frei Caneca in the Atlantic rain forest of Pernambuco, Brazil.

averaged over 47 years at Frei Caneca, which is 7 km from the reserve, is 1332 mm (unpublished meteorological data provided by Usina Colônia).

Sampling of Sphingidae. The survey was undertaken between August 2003 and July 2004. A 250W mercury-vapor light source, positioned against a white wall of the Reserve Station inside the park facing the forest, was used to attract moths. Specimens were collected on two consecutive new moon nights per month from 18.00h to 5.00h of the following day. Moths were killed by an injection of ethyl acetate in the posterior part of the thorax. Each specimen was then placed in an entomological envelope and prepared in the laboratory.

Moths were identified using d'Abrera (1986) and Kitching & Cadiou (2000) and the reference collection at UFPE. Specimens were deposited in the Entomological Collection of the Federal University of Pernambuco (UFPE, Recife) and the Entomological Collection of the Department of Systematics and Ecology, Federal University of Paraíba (UFPB, João Pessoa).

Three abundance criteria were established using Rabinowitz *et al.* (1986), based on the number of specimens collected per species: rare (1 to 2), common (3 to 19), and abundant (20 to 50).

Bio-Estat 2.0 (Ayres *et al.* 2000) was used to calculate Pearson's correlation coefficients (Sokal & Rohlf 1996). The data were adjusted to lognormal distributions according to the model of Preston (1948), which groups the species into frequency classes of individuals on a logarithmic scale. The program "lognorm.bas" (Ludwing & Reynolds 1988) was used, according to the equation $S(R)=S_0e^{(a^2R^2)}$, where $S(R)$ is the estimated number of species in a given octave, R is the distance in relation 1,2,3,.. (Octaves), S_0 is the estimated number of species in the modal octave, e is the natural logarithm base, and a an estimated constant calculated as $a^2 = 1/(2s)^2$, where s is the standard deviation. Dates were compared with regional inventories of Sphingidae of the Amazonian rain forest, south Atlantic rain forest and caatinga. Similarities were analyzed using NTSYS pc version 2.10t.

RESULTS

Three hundred and seventy-nine individuals, representing 50 species in 19 genera were recorded, of which 15 species are new records for northeast Brazil (Table 1). The most abundant species were *Erinnyis ello* Linnaeus 1758, *Erinnyis alope* (Drury 1773), *Neogene dynaeus* (Hübner [1825]) and *Protambulyx astygonus* (Boisduval [1875]), accounting together for 44.2% of the individuals recorded. Only 1 or 2 individuals were recorded for 17 species (Fig. 2).

From October to December, the driest months of the study period (192 mm, 6.6% of total rainfall), 170

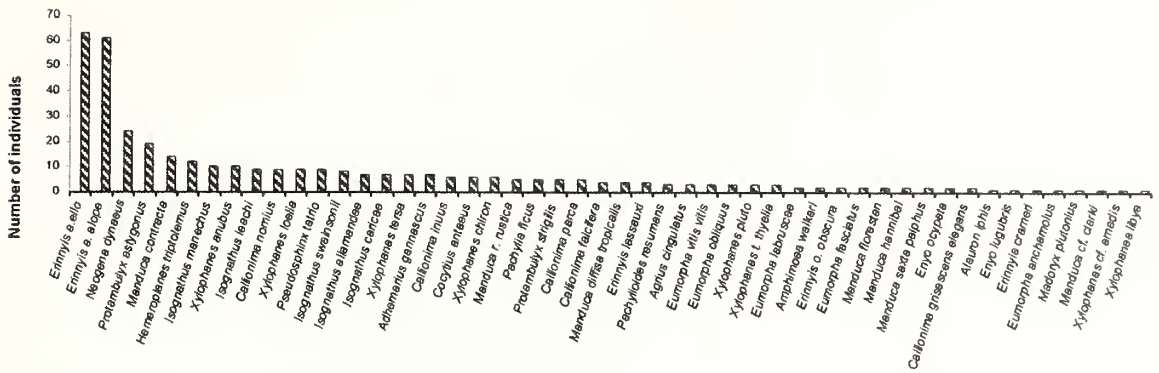

FIG. 2. Number of individuals of sphingid species recorded from August 2003 to July 2004 in the Atlantic rain forest of Frei Caneca, Pernambuco

individuals were recorded, 45% of the total. In January, the month with the highest rainfall (554 mm, 19%), only 2 individuals were recorded, *Adhemarius gannascus* (Stoll 1790) and *Protambulyx astygonus* (Boisduval [1875]). Other months with high rainfall, namely May, June and July (1120 mm, 392%) also showed low hawkmoth abundance (70 individuals, 18.5%). More than half of the species (30 individuals, 58.8%) were recorded in March (Table. 1).

The male to female sex ratio was 4:1, with 80% of captured moths being males. For almost half the species (26/50) only males were recorded. In the north Atlantic rain forest, species richness is lower in the rainy months. Pearson's correlation coefficient between rainfall 2003/2004 and abundance was -0.6813, and between rainfall 2003/2004 and species richness was -0.6741, both negative and significant (< 0,05). The species accumulation curve (Fig. 4), shows that by the fifth month of collecting 70.5% of the total number of sphingid species had been recorded and after the tenth month the number of species did not increase. The estimated number of species in the study area was 52 (Fig. 5).

DISCUSSION

The sphingid fauna of the north Atlantic rain forest shows a much higher species richness and abundance than that found in another survey, undertaken in the Atlantic rain forest, Nature Reserve of Gurjaú in Pernambuco, using the same methodology and the same sampling effort, in which only 23 species were recorded (Duarte & Schlindwein 2005a). Of these, only *Pachylia syces*, *Protambulyx eurycles*, *P. goeldii* and *Manduca brasilensis* were not recorded in the present study. The Nature Reserve, Frei Caneca is only 150 km distant from the reserve Gurjaú and is characterized by a little disturbed rain forest in a good level of conservation. The latter area is heavily fragmented, close to the metropolitan area of Recife City, surrounded and strongly impacted by sugar cane monocultures. The high number of additions to the list of the northeast Brazilian sphingid fauna (15 species) shows that the sphingid fauna of this area is still poorly known. No surveys are available for any other northeast Brazilian states (Bahia, Sergipe, Alagoas, Ceará, Piauí and Maranhão). These would most likely further increase the number of species in this region. Our study corrects earlier statements made about the apparently restricted distributions of some species, such as *Xylophanes anubus*, *Amphimoea walkeri* and *Madoryx plutonius*, which are now known to be more widespread in the neotropical region than previously thought.

The sphingid fauna of the Atlantic rain forest of Pernambuco shows no strong seasonal pattern, but we found a significant negative correlation between rainfall and both species richness and abundance, such that the rainiest months showed the lowest species richness and abundance. In Costa Rica adult sphingids were almost absent at the end of the dry season, abundant in the rainy season but scarce in October, the most humid month of the year. Abundance of Sphingidae was associated with the presence of leaves on their larval host-plants (Haber & Frankie 1989). In the south Brazilian state of Paraná, which is outside the tropics, sphingid abundance was correlated with temperature and abundance drastically diminished in winter (Marinoni *et al.* 1999). The sphingid fauna is also highly seasonal in the dry northeast Brazilian caatinga, where greatest abundance is in March at the beginning of the rainy season, when larval host-plants provide their leaves (Duarte & Schlindwein 2005b). Similar results were found in Mexico, where 77% of sphingids were recorded only in the rainy season (Gómez-Nucamendi *et al.* 2000).

TABLE 1. Species of Sphingidae recorded in the Atlantic rain forest of Frei Caneca, Pernambuco, Brazil, from August 2003 to July 2004. The abundance categories follow Rabinowitz *et al.* (1986).

Taxon	Month	Rare	Common	Abundant	Male	Female	Total
Macroglossinae							
MACROGLOSSINI							
Xylophanes cf. amadis (Stoll, 1782)	Aug	x			1	0	1
Xylophanes anubus (Cramer, 1777) °	Feb-May, Jun		x		9	1	10
Xylophanes pluto (Fabricius, 1777)	Mar, Nov		x		3	0	3
Xylophanes t. tersa (Linnaeus, 1771)	Apr, May, Aug, Nov, Dec		x		5	2	7
Xylophanes chiron (Drury, 1773) °	Mar, Sep, Oct Dec			x	6	0	6
Xylophanes libya (Druce, 1878)	Sep	x			1	0	1
Xylophanes loelia (Druce,1878)	Fev, Mar-Jun, Oct		x		8	1	9
Xylophanes t. thyelia (Linnaeus, 1758) °	Mar, Oct, Dec		x		3	0	3
DILOPHONOTINI							
Aleuron iphis (Walker, 1856) °	May	x			1	0	1
Callionima falcifera (Gehlen,1943) °	Mar, Dec		x		4	0	4
Callionima grisescens elegans (Gehlen,1935)	Feb	x			1	1	2
Callionima innus (Rothsch. & Jordan, 1903) °	Mar, May, Jun, Oct, Dec		x		4	2	6
Callionima nomius (Walker, 1856) °	Feb-Apr, May, Dec		x		8	1	9
Callionima parce (Fabricius, 1775)	Feb, Mar, May, Aug, Nov		x		4	1	5
Erinnyis a. alope (Drury, 1773)	Feb-Apr, Sep-Dec			x	50	11	61
Erinnyis crameri (Schaus, 1898)	Aug	x			1	0	1
Erinnyis e. ello (Linnaeus, 1758)	Mar-Jun, Sep-Dec			x	37	26	63
Erinnyis lassauxii (Boisduval, 1859)	Mar, May		x		4	0	4
Erinnyis o. obscura (Fabricius, 1775)	Mar	x			2	0	2
Enyo l. lugubris (Linnaeus, 1771)	Sep	x			1	0	1
Enyo ocypete (Linnaeus, 1758)	May	x			2	0	2
Hemeroplanes triptolemus (Cramer, 1779)	Feb, May, Jun, Sep, Nov, Dec		x		9	3	12
Isognathus allamandae Clark, 1920	May, Jun, Oct, Dec		x		7	0	7
Isognathus c. caricae (Linnaeus, 1758)	Feb-May, Oct, Dec		x		7	0	7
Isognathus leachii (Swainson, 1823)°	Feb -Jun, Dec		x		7	2	9
Isognathus menechus (Boisduval, [1875])	Feb-May, Sep, Dec		x		8	2	10
Isognathus swainsonii (Felder & Felder, 1862)°	Mar,Oct, Nov		x		8	0	8
Madoryx plutonius (Hübner, [1819])°	Oct	x			1	0	1
Pachylia ficus (Linnaeus, 1758)	May, Oct, Nov		x		2	3	5
Pachylioides resumens (Walker, 1856) °	May	x			2	1	3
Pseudosphinx tetrio (Linnaeus, 1771)	Feb, Mar, Sep-Dec		x		7	2	9
PHILAMPELINI							
Enmorpha anchemolus (Cramer, 1779)	Nov	x			1	0	1
Eumorpha f. fasciatus (Sulzer, 1776)	Apr, May	x			2	0	2
Enmorpha l. labruscae (Linnaeus, 1758)	May	x			0	2	2
Eumorpha obliquus (Rothsch & Jord, 1903) °	Mar, Oct, Dec		x		3	0	3
Enmorpha v. vitis (Linnaeus, 1758)	Mar, Apr	x			3	0	3

TABLE 1. Continued.

Taxon	Month	Rare	Common	Abundant	Male	Female	Total
Smerinthinae							
AMBULYCINI							
Adhemarius gannascus (Stoll, 1790)	Jan-May, Dec		x		6	1	7
Protambulyx strigilis (Linnaeus, 1771)	May, Nov, Dec		x		5	0	5
Protambulyx astygonus (Boisduval, [1875])	Jan-Mar, Oct-Dec		x		18	1	19
Sphinginae							
SPHINGINI							
Agrius cingulatus (Fabricius, 1775)	Jun, Sep	x			2	1	3
Amphimoea walkeri (Boisduval, [1875]) °	Mar, Jun	x			2	0	2
Cocytius antaeus (Drury,1773)	Mar-May, Oct		x		4	2	6
Neogene dynaeus (Hübner, [1825])	Feb-Jun, Aug-Dec			x	20	4	24
Manduca cf. clarki (Rothsch. & Jordan, 1916)	Mar	x			1	0	1
Manduca contracta (Butler, 1875) °	Feb, Mar, May, Jun		x		12	2	14
Manduca diffissa tropicalis (Rothsch. & Jord, 1903)	Mar, Sep., Oct		x		4	0	4
Manduca h. hannibal (Cramer,1779)	May, Nov	x			1	1	2
Manduca florestan (Stoll, 1782) °	Mar, Apr	x			2	0	2
Manduca r. rustica (Fabricius, 1775)	Feb, Sep, Dec		x		4	1	5
Manduca sexta paphus (Cramer, 1779)	Mar	x			1	1	2
Total					**304**	**75**	**379**

°New occurrence in northeastern Brazil

TABLE 2. Presence of sphingid species in the northern Atlantic rain forest (this study), Amazonian rain forest (Motta *et al.* 1998; Motta & Andreazze 2002), southern Atlantic rain forest (Laroca & Mielke 1975, Marinoni *et al.*1999) and caatinga (Duarte *et al.* 2001, Gusmão & Creão-Duarte 2004, Duarte & Schlindwein 2005b).

Taxon	N-Atlantic Rainforest	Amazonian Rainforest	S-Atlantic Rainforest	Caatinga
Adhemarius gagarini (Zikan, 1935)		x		
Adhemarius gannascus (Stoll, 1790)	x	x	x	
Adhemarius palmeri (Boisduval, 1875)		x	x	
Aellopos ceculus (Cramer, 1777)		x		
Agrius cingulatus (Fabricius, 1775)	x	x	x	x
Aleuron chloroptera (Perty, 1834)		x		
Aleuron iphis (Walker, 1856)	x	x		
Aleuron n. neglectum (Rothschild & Jordan, 1903)		x		
Amphimoea walkeri (Boisduval, [1875])	x	x		
Callionima falcifera (Gehlen, 1943)	x			
Callionima grisescens elegans (Gehlen, 1935)	x			x
Callionima inuus (Rothschild & Jordan, 1903)	x	x	x	
Callionima nomius (Walker, 1856)	x	x	x	
Callionima p.pan (Cramer, 1779)		x		
Callionima parce (Fabricius, 1775)	x	x	x	x
Cocytius antaeus (Drury, 1773)	x	x	x	x
Cocytius beelzebuth (Boisduval, 1875)			x	
Cocytius duponchel (Poey, 1832)		x	x	
Cocytius lucifer (Rothschild & Jordan, 1903)			x	
Enyo g.gorgon (Cramer, 1777)		x	x	
Enyo l. lugubris (Linnaeus, 1771)	x	x	x	x
Enyo ocypete (Linnaeus, 1758)	x	x	x	
Erinnyis a. alope (Drury, 1773)	x	x	x	x
Erinnyis crameri (Schaus, 1898)	x	x	x	
Erinnyis e. ello (Linnaeus, 1758)	x	x	x	x
Erinnyis lassauxii (Boisduval, 1859)	x	x	x	x
Erinnyis o. obscura (Fabricius, 1775)	x	x	x	x
Erinnyis oenotrus (Stoll, 1780)		x	x	
Eumorpha anchemolus (Cramer, 1779)	x	x	x	
Eumorpha capronnieri (Boisduval, 1875)		x		
Eumorpha eacus (Cramer, 1780)		x		
Eumorpha f. fasciatus (Sulzer, 1776)	x	x		x
Eumorpha l. labruscae (Linnaeus, 1758)	x	x	x	x
Eumorpha obliquus (Rothschild & Jordan, 1903)	x	x	x	
Eumorpha phorbas (Cramer, 1775)		x		
Eumorpha v. vitis (Linnaeus, 1758)	x	x	x	x
Eupyrrhoglossum venustum (Rothschild & Jordan, 1903)		x		
Hemeroplanes triptolemus (Cramer, 1779)	x	x	x	
Hyles euphorbiarum (Guérin & Percheron, 1835)				x
Isognathus allamandae Clark, 1920	x	x		
Isognathus australis Clark, 1917				x
Isognathus c. caricae (Linnaeus, 1758)	x	x		
Isognathus excelsior Boisduval, 1875		x		
Isognathus leachii (Swainson, 1823)	x	x		
Isognathus m. mossi Clark, 1917		x		

TABLE 2. Continued.

Taxon	N-Atlantic Rainforest	Amazonian Rainforest	S-Atlantic Rainforest	Caatinga
Isognathus menechus (Boisduval, [1875])	x			x
Isognathus rimosus (Grote, 1865)		x		
Isognathus scyron (Stoll, 1780)		x		
Isognathus swainsonii (Felder & Felder, 1862)	x	x		
Isognathus zebra Clark, 1923		x		
Madoryx plutonius (Hübner, [1819])	x	x	x	
Manduca brasilensis Jordan, 1911	x			x
Manduca brunalba (Clark, 1929)		x		
Manduca cf. clarki (Rothschild & Jordan, 1916)	x	x		
Manduca lucetius (Cramer, 1780)		x		
Manduca contracta (Butler, 1875)	x			
Manduca d. dalica (Kirby, 1877)		x		
Manduca diffissa tropicalis (Roth. & Jordan, 1903)	x	x	x	
Manduca florestan (Stoll, 1782)	x	x	x	
Manduca h. hannibal (Cramer, 1779)	x	x	x	
Manduca l. lefebvrei (Guérin, 1844)		x	x	
Manduca p. pellenia (Herrich-Schaeffer, 1854)		x	x	
Manduca r. rustica (Fabricius, 1775)	x	x	x	x
Manduca sexta paphus (Cramer, 1779)	x	x	x	x
Neococytius cluentius (Cramer, 1775)		x	x	
Neogene dynaeus (Hübner, [1827]-[1831])	x			x
Nyceryx c. continua (Walker, 1856)			x	
Orecta l. lycidas (Boisduval, 1875)			x	
Oryba kadeni (Shaufuss, 1870)		x		
Pachylia darceta Druce, 1881		x		
Pachylia ficus (Linnaeus, 1758)	x	x	x	
Pachylia syces (Hübner, [1819])	x			
Pachylioides resumens (Walker, 1856)	x	x	x	
Perigonia lusca lusca (Fabricius, 1777)				x
Perigonia pallida Rothschild & Jordan, 1903				x
Perigonia pittieri Lichy, 1962				x
Phryxus caicus (Cramer, 1777)		x		
Protambulyx astygonus (Boisduval, [1875])	x			
Protambulyx curycles (Roth. & Jordan, 1903)	x	x		
Protambulyx goeldii (Roth. & Jordan, 1903)	x			
Protambulyx strigilis (Linnaeus, 1771)	x	x	x	x
Pseudosphinx tetrio (Linnaeus, 1771)	x	x	x	x
Xylophanes aglaor (Boisduval, 1875)			x	
Xylophanes amnbus (Cramer, 1777)	x	x	x	
Xylophanes ceratomioides (Grote & Robinson, 1867)			x	
Xylophanes cf. amadis (Stoll, 1782)	x	x		
Xylophanes chiron (Drury, 1773)	x	x	x	
Xylophanes indistincta Closs, 1915			x	
Xylophanes isaon (Boisduval, 1875)			x	
Xylophanes libya (Druce, 1878)	x			
Xylophanes loelia (Druce, 1878)	x	x		
Xylophanes pluto (Fabricius, 1777)	x		x	x
Xylophanes porcus continentalis Rothschild & Jordan, 1903		x	x	
Xylophanes s. schausi (Rothschild, 1894)			x	
Xylophanes t. tersa (Linnaeus, 1771)	x	x	x	x
Xylophanes t. thyelia (Linnaeus, 1758)	x	x	x	
Xylophanes titana (Druce, 1878)			x	
Xylophanes tyndarus (Boisduval, 1875)			x	
Xylophanes xylobotes (Burmeister, 1878)			x	
Total	54	71	63	26
Species in common with the N-Atlantic Rain Forest		42 (59 %)	32 (58%)	20 (77%)

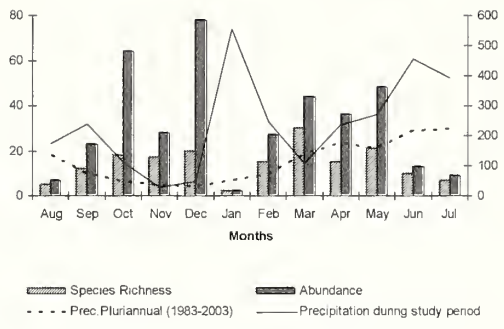

FIG. 3. Abundance and richness of sphingids, mean annual precipitation and precipitation during the study period in the Atlantic rain forest of Frei Caneca from August 2003 to July 2004.

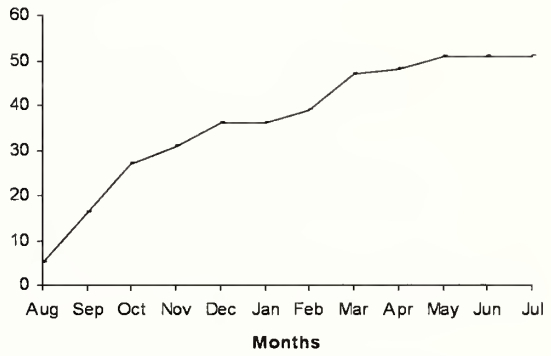

FIG. 4. Species accumulation curve of Sphingidae during the study, from August 2003 to July 2004, in the Atlantic Rain Forest of Frei Caneca.

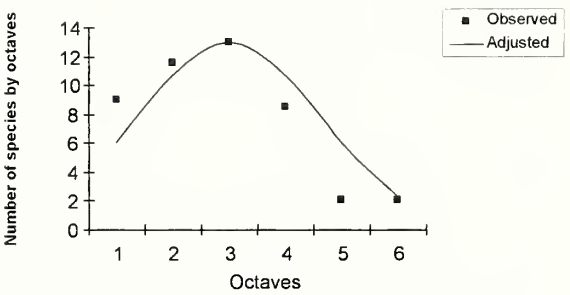

FIG. 5. Distribuition of species recorded in the Atlantic rain forest of Frei Caneca by abundance class (octaves), adjusted to a lognormal curve.

In the north Atlantic rain forest, the vegetation is not deciduous and host-plants have leaves throughout the year, a factor that probably exercises great influence on the sphingid abundance. In Pará (Amazonian region), Moss (1920) noted that periods of heavy rainfall reduced the abundance of hawkmoths, because they dislodged larvae, mainly those newly-emerged from the egg.

Callionima grisescens elegans is a sphingid subspecies endemic to northeast Brazil (Schreiber 1978), occurring abundantly in the caatinga (Duarte & Schlindwein 2005b) and tropical montane forest in Paraíba (Gusmão & Creão-Duarte 2004). In the Atlantic rain forest, only two specimens were recorded, suggesting that it is a resident species of the caatinga.

The high male to female ratio in our study follows a pattern similar to the 10:1 male to female capture ratio reported in Costa Rica by Janzen (1983). The expected male to female proportion is 1:1 (Kitching & Cadiou 2000). It appears that sampling of sphingids with light traps distorts this ratio. Janzen (1983) supposed that the two sexes could have a physiological susceptibly to light, with males showing a high mobility using light sources as reference points in finding females.

Comparison of the present short-term survey of the sphingid fauna of the northern Atlantic rain forest with those conducted in the southern Atlantic rain forest (Laroca & Mielke 1975, Marinoni *et al.* 1999), caatinga (Gusmão & Creão-duarte 2004, Duarte & Schlindwein 2005b) and the Amazonian forest (Motta *et al.* 1998; Motta & Andreazze 2002) showed that 78% (42) of the species recorded in the northeastern Atlantic rain forest also occur in the Amazonian forest, 59% (32) in the southern Atlantic rain forest, and 37% (20) in the caatinga. *Protambulyx astygonus*, *Callionima falcifera*, *Pachylia syces*, *Manduca contracta* and *Xylophanes libya* were recorded only in the northeastern Atlantic rain forest (Table 2). Nevertheless, these comparisons have to be treated with care, because the compiled species lists of all regions are results of short-term surveys.

The present study shows that the sphingid fauna of the north Atlantic rain forest is most similar to that of the Amazonian forest when compared to other regions. Several authors have demonstrated a close faunistic and floristic relationship between these two forests (Andrade-Lima 1982, Bigarella *et al.* 1975, Vanzolini 1970, Haffer 1982, Santos *et al.* 2007), which today are separated by about 1500 km. The xeromorphic caatinga forest, that occupies the gap between the rain forests, is characterized by a highly endemic flora (Queiroz *et al.* 2006). The sphingid fauna of the caatinga, however, is impoverished and formed almost exclusively from

elements of the Atlantic and the Amazonian rain forests.

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NOTES ON *PAPILIO MACHAON ALIASKA* (PAPILIONIDAE) POPULATIONS NEAR FAIRBANKS, AK

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ABSTRACT. I present results from a mark-recapture study of *Papilio machaon aliaska* swallowtail butterflies from four sites near Fairbanks, Alaska. The sites were alpine-tundra hilltops and butterflies were caught throughout the month of June in 2000–2003. Only males (n=569) were marked and released while females (n=31) were kept for other experiments. Adult males tended to fly earlier in the season than did females and also were found flying earlier in the day than females. About one sixth of the males that were marked were later recaught and some were caught multiple times (up to six times for one male). Most males were recaught within four days of their initial catch date, but a few were caught many days later. Thus, these data indicate that some males may live for up to two to three weeks under natural field conditions. The research presented here support the claim that *P. m. aliaska* is a hilltopping swallowtail butterfly.

Additional key words: flight behavior, flight times, mark-recapture.

Swallowtail butterflies from the *Papilio machaon* group use plants of the Apiaceae as their primary hosts (Feeny *et al.* 1983; Sperling 1987; Thompson 1995; Wiklund 1981). Apart from occasional use of plants in the family Rutaceae, an ancestral host family for the genus *Papilio* (Sperling 1987), *P. machaon* swallowtails have rarely incorporated non-apiaceous plants into their diet. In Alaska and northwestern Canada, *Papilio machaon aliaska* Scud. oviposits and feeds not only on the local apiaceous host, *Cnidium cnidiifolium* (Turcz.) Schischk., but also on *Artemisia arctica* Less. and *Petasites frigidus* (L.) Franch. (Scott 1986) in the Asteraceae. This host-range expansion by *P. m. aliaska* appears to represent an intermediate step towards a complete host shift.

Previous work has demonstrated that shared chemical cues in ancestral and novel host plants may have provided the opportunity for the establishment of the host expansion onto the two novel host species (Murphy & Feeny 2006). However, these host plants are not equal in terms of larval survival in the field (Murphy 2004) or the laboratory (Murphy 2007a). In the absence of predators, *P. m. aliaska* larvae survive best on the ancestral host plant, *C. cnidiifolium*, but in the presence of predators, larval survival is greater on the novel host plants. In the field, the novel host plants seem to offer larvae enemy-free space that is not found on the ancestral host plant simply because of their different local environments. Predators are common in the ancestral host plant's environment and larval mortality on *C. cnidiifolium* can be very high in the field; enemy-free space on the novel host plants may be the selective pressure maintaining the host expansion, possibly driving the incipient host shift to completion.

Despite the environmental differences and physical distance between the locations where the larval host plants can be found, *P. m. aliaska* is thought to be a typical hilltopping swallowtail butterfly (cf. Lederhouse 1982; Shields 1967). Hilltopping is a widespread behavior in butterflies and has been documented in at least five Lepidoptera families, including Papilionidae (Shields 1967). When males and virgin females emerge from their pupae, they fly towards a local topographic prominence (Pe'er *et al.* 2004), which may be quite minor in appearance (Baughman & Murphy 1988), and congregate at the summit. Hilltopping behavior may be an effective method for finding mates in low-density species (Scott 1968) or in species that do not mate on or near their larval host plants (Rutowski 1991). Males tend to establish territories (or 'perches' *sensu* Scott 1974) and exhibit aggressive behaviors towards other males as well as other butterfly species (Lederhouse 1982). Virgin females, or females that mate multiple times in some species, also summit the hilltop, mate with the males, and then return to lower elevations to search for oviposition sites (Shields 1967, but see Pe'er (2004) for a discussion of whether this downhill movement is active or passive). Thus, on these hilltops, males tend to be numerically more common than are females since females only summit long enough to mate while males defend their territories and wait for new mates at the top of the hill (Alcock 1985; Shields 1967). Lederhouse (1982) found that for the black swallowtail butterfly, *Papilio polyxenes*, early-emerging males were more likely to defend a preferred territory, and these preferred territories were visited more frequently by females.

Here I present data that I gathered when I was collecting *P. m. aliaska* individuals in the field, including a mark-recapture study on *P. m. aliaska* males. The goal of this research is to investigate the flight behaviors of *P. m. aliaska* butterflies in the field. In addition to learning

more about peak flight time and longevity under natural conditions, I aimed to determine if my observations of *P. m. aliaska* flight behavior near Fairbanks, AK are consistent with patterns associated with other hilltopping butterflies (e.g. female rarity and males that either remain or return to a hilltop regularly for several days).

MATERIALS AND METHODS

With help from many field assistants, I collected *P. m. aliaska* individuals from four sites in Alaska. The sites were alpine-tundra hilltops (domes) near Fairbanks, AK: Ester Dome (64°52'N, 148°4'W, ~720m), Murphy Dome (64°57'N, 148°21'W, ~890m), Wickersham Dome (65°13' N, 148°3' W, ~977m) and along the Pinnel Mountain trail southwest of Table Mountain (65°25' N, 145°57' W, ~1,200m). The two closest sites, Ester and Murphy domes, are about 18 km apart while the two sites that are farthest from each other are about 120 km apart (Ester and Pinnel Mountain). These four sites have populations of the host plants *Artemisia arctica* and *Petasites frigidus* and vegetation characteristic of open tundra. Ester and Murphy Domes are characterized by low birch and willow scrub (*Betula, Salix* spp.) with a few small spruces (*Picca*) as well as dwarf scrub (*Andromeda, Anemone, Carex, Empetrum, Epilobium, Ledum, Lupinus, Pedicularis, Petasites, Pyrola, Salix, Vaccinium, Valariana*). The Pinnel Mountain trail and Wickersham Dome are more open, without any trees on the tops of the domes, and the terrain is covered by the dwarf scrub described above.

In 2000 I was the only person in the field collecting butterflies. In 2001 and 2002, however, I had a field assistant so the number of butterflies caught reflects the efforts of two people. During these two field seasons I would often drop my assistant off at one dome and then I would travel to another dome. We were thus sampling two sites per day, each with the effort of a single person. In 2003 I had two field assistants, but this year we all sampled a single site together. We spread out and were able to sample each site more extensively. During each field season, we began searching for butterflies by May 25 and continued searching for flying adults until early July. All butterflies that were caught were marked and numbered (see Carter & Feeny 1985) and during the 2001, 2002 and 2003 field seasons the time of day that the butterflies were caught was also recorded. Females were kept for experiments. Most males were released at the end of the day although some were kept overnight so that we could mate them with the females. The males that were kept were released within a day or two and always at the same field site.

Sampling effort varied by site; the sites that were closer to Fairbanks (Ester Dome and Murphy Dome) were sampled more frequently than the sites that were more distant (Pinnel Mountain and Wickersham Dome). Ester Dome was sampled a total of 25 days (5 days in 2000, 6 days in 2001, 8 days in 2002 and 6 days in 2003). Murphy Dome was sampled a total of 18 days (4 days in 2000, 4 days in 2001, 6 days in 2002 and 4 days in 2003). Pinnel Mountain was sampled a total of 6 days (3 days in 2000, 2 days in 2001 and 1 day in 2003). Wickersham Dome was sampled a total of 11 days (4 days in 2000, 4 days in 2001, 1 day in 2002 and 2 days in

TABLE 1. Number of male and female *P. m. aliaska* individuals collected at each field site during each year of the study.

	Site				
Year	Ester Dome	Murphy Dome	Pinnel Mtn	Wickersham Dome	Totals
Females					
2000	1		2	4	7
2001	4	2	3	1	10
2002		2			2
2003	6	1		5	12
Totals	11	5	5	10	**31**
Males					
2000	14	62	26	23	125
2001	26	22	27	49	124
2002	53	71		34	158
2003	32	76	7	47	162
Totals	125	231	60	153	**569**

2003). The sites were visited more frequently than the number of days given above, but only days in which butterflies were actually caught are counted in the tallies.

RESULTS AND DISCUSSION

Males were plentiful and easy to find and catch. During the four years of data presented here, we caught 569 males (Table 1). Males were often observed circling an object (a bush, rock or piece of debris) as well as other males that approached. Females were more difficult to find. Over the four years of data presented here, we collected only 31 females (Table 1). I do not think that this reflects a skewed sex ratio as I have reared the progeny of both wild-caught and lab-reared females and the sex ratio of their offspring has never been significantly different from 50:50 (S. Murphy, unpublished data). Rather, the difference in the number of males and females caught probably represents a difference in their behaviors; indeed female rarity is common at hilltop sites in other hilltopping butterflies (Shields 1967). My observations of how rare females are on the hilltops is consistent with the notion that females only stay on top of the domes long enough to mate and then they fly downhill towards larval host plant sites. Once my field assistants and I had caught all of the males that were present on a dome upon our arrival, new males were observed flying up from lower elevations and they began to occupy the newly unoccupied perches. Given the difficulty in accessing some of the field sites, we were not able to sample every site every day. Hence, any females that arrived on days that we were not present were able to mate and fly away without our having ever encountered them. However, any males that arrived at a site on a day that we were not present were likely caught the next time we visited that site given their propensity to remain on the hilltops. For these reasons, I feel that my data are a rather accurate representation of the number of males that were present at these dome sites, but that the number of females has been significantly underestimated simply because their behavior makes them more difficult to catch when we could not be present at every dome site everyday.

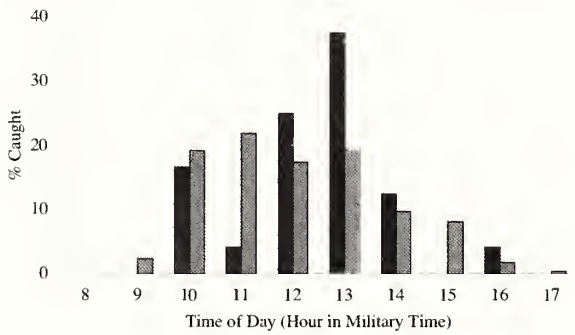

FIG. 1. Female (black bars) and male (gray bars) *Papilio machaon aliaska* butterflies that were caught during each hour of the day given as a percentage of the total caught. The data is given for all four field sites combined, but only for butterflies caught during the 2001–2003 field seasons (Females n=24; Males n=444).

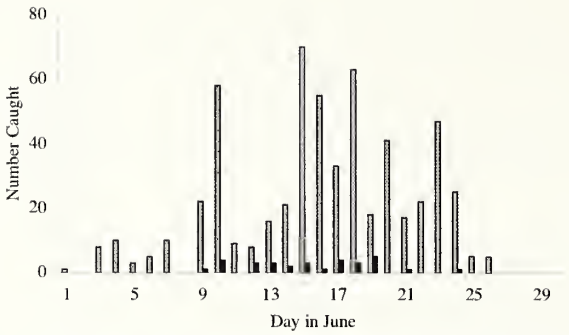

FIG. 2. Number of female (black bars) and male (gray bars) *Papilio machaon aliaska* butterflies that were caught during the month of June for all years (2000–2003).

I was able to find both males and females at each of the four sites described in the methods section above (Table 1). Males tend to be caught earlier in the day than females (Fig. 1), although none was ever caught before 9:00 hr. Their peak flight time was between 11:00-12:00 hr while the majority of females was caught slightly later, between 13:00–14:00 hr, but these two distributions for flight time did not differ significantly ($P > 0.1$, Wilcoxon signed-rank test on ranks). Females were never caught before 10:00 hr. Females also were caught a few days later than the first males were caught (Fig. 2). The earliest females were caught on June 9 while the latest females were caught on June 24. The earliest male was caught on June 1 while the latest male was caught on June 26.

Nearly 17% of the males (n=96) were recaught at the same field site during a subsequent visit (Fig. 3); males were never found to have traveled between sites, which is not surprising given the significant distances between them. The majority of these males were only recaught once, but a few were caught several times. One male was recaught six times in the same location on a dome, which I interpret to mean that he was occupying the same perch or territory for several days. Most males were recaught within four days of their initial catch date. A few, however, were caught many days later. This gives us some insight as to how long males can live in the field. For instance, at least one male lived a minimum of 18 days in the field.

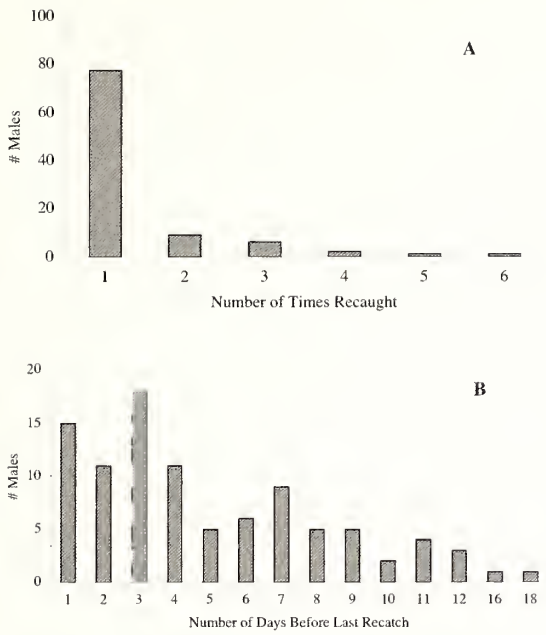

FIG. 3. Many male *Papilio machaon aliaska* butterflies (n=96) were caught, marked and released and then re-caught during this study (2000–2003). Of these males that were re-caught, many were caught multiple times. A) The number of times that the marked males were re-caught. B) The number of days that passed between the first time a male butterfly was caught and the last time he was caught.

Although not directly tested, my observations are consistent with the idea that males tend to establish territories at the top of the dome that they then occupy, as evidenced by the number of males that were recaught on the domes along with personal observations of their behavior before they were caught. Males tend to emerge earlier in the season than do females and also fly earlier in the day than females. Finally, while males are commonly found on the hilltops, females are rarer. Together, these data support the claim that *P. m. aliaska* is a hilltopping swallowtail butterfly.

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DIFFERENTIAL ANTENNAL SENSITIVITIES OF THE GENERALIST BUTTERFLIES *PAPILIO GLAUCUS* AND *P. CANADENSIS* TO HOST PLANT AND NON-HOST PLANT EXTRACTS

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ABSTRACT. It is likely that olfaction is used by some generalist insect species as a pre-alighting cue to ameliorate the costs of foraging for suitable hosts. In which case, significantly higher antennal sensitivity would be expected to the volatiles of preferred over less or non-preferred host plants. To test this hypothesis, antennal sensitivity was measured by recording electroantennogram (EAG) responses from intact antennae of the generalists *Papilio glaucus* L. and *P. canadensis* R & J (Papilionidae) to methanolic leaf extracts of primary, secondary, and non-host plants. EAGs recorded from antennae of *P. glaucus* were approximately four fold higher than those of *P. canadensis* in response to extracts of its most suitable host plant, *Liriodendron tulipifera* (Magnoliaceae). Likewise, EAG responses of *P. canandensis* to its preferred host, *Populus tremuloides* (Salicaceae), were significantly higher than those of *P. glaucus*. In addition, *P. glaucus* exhibited significantly higher (approximately three fold) EAG responses to its preferred host, *L. tulipifera*, than to its less-preferred hosts, *Ptelea trifoliata*, *Sassafras albidum*, and *Lindera benzoin*. The results from this study indicate a significant divergence in the olfactory system of two closely related generalist butterfly species, including a strong specialization in the olfactory system of *P. glaucus*.

Additional key words: Electroantennogram, olfaction, oviposition, decision-making, host selection.

For insects with larvae that develop on a single host plant, female ovipositional choice determines larval habitat and therefore the likelihood of larval survival. However, a clear correlation between adult ovipositional preference and host suitability for larval growth has not been found in many systems (reviewed in Mayhew 1997), and 'mistakes' in which eggs are laid on plants toxic to the larvae are fairly common (Straatman 1962; Wiklund 1975; Chew 1977; Berenbaum 1981; Larsson & Ekbom 1995; Renwick 2002; Graves & Shapiro 2003). Such 'mistakes' are believed to be rare for phytochemically specialized species, but generalists, such as *Papilio glaucus* L. and *P. canadensis* R & J (Papilionidae), are known to regularly place a small fraction of their eggs on hosts toxic to their larvae in natural habitats (Brower 1958, 1959) and in controlled environments despite the presence of a suitable alternative (Scriber *et al.* 1991; Scriber 1993). In contrast, specialist herbivores may fail to oviposit on readily available suitable hosts; for example, *Papilio palamedes*' geographic range is determined by female ovipositional preference and not the availability of hosts suitable for larval development (Lederhouse *et al.* 1992). One hypothesis that has been proposed to explain this observation and the higher abundance of specialist insects is that an increase in error rate should be associated with an increase in polyphagy (Levins & MacArthur 1969). In recent years this idea has been updated in terms of neural limitations to include a prolonged decision-making time along with an increased error rate as costs of polyphagy (Bernays 2001; Janz 2003).

Despite the common assertion that olfaction is an important sensory modality for orientation to host plants (Renwick & Chew 1994; Dicke 2000; Finch & Collier 2000), the importance of olfactory cues for oviposition-site location in day-flying butterflies has received relatively little attention compared with moths (reviewed in Hansson 1995; Honda 1995, but see Feeny *et al.* 1989; van Loon *et al.* 1992; Baur & Feeny 1995; Kroutov *et al.* 1999). In addition, the role of olfactory cues in butterfly host plant searching and acceptance behavior has received little attention relative to visual and/or contact cues (e.g. Rausher 1978; Stanton 1982; Scherer & Kolb 1987; Grossmueller & Lederhouse 1985; Thompson & Pellmyr 1991; Honda 1995; Weiss 1997; Schoonhoven *et al.* 1998).

Olfactory cues may play an important role in long and short-range searching behavior of pre-alighting generalist butterflies increasing their efficiency. Baur & Feeny (1995) found electroantennogram (EAG) evidence for evolutionary lability in the peripheral

olfactory system of three specialist butterflies, *Papilio* polyxenes, *P. machaon hippocrates*, and *P. troilus*. If the peripheral olfactory system is labile, it may allow for adaptations in generalist species that allow for a functionally specialized behavior in areas where a primary host is abundant, while maintaining the flexibility to accept alternate hosts in areas where the primary host(s) are rare or not present. If olfactory cues are used to reduce decision-making time in generalist species, significantly higher sensitivity would be expected in the peripheral nervous system to primary hosts over less preferred hosts.

We tested this hypothesis for the polyphagous *P. glaucus* by comparing its antennal sensitivity by EAG recordings with that of its sibling species, *P. canadensis*, to extracts of preferred, secondary, and non-host plants. These two sister species can readily produce fertile hybrid offspring (e.g. Scriber 1998); *P. canadensis* males prefer *P. glaucus* females (Deering & Scriber 2002), and until recently, they were considered the same species (Hagen *et al.* 1991). However, despite their similarities they exhibit significant differences in host plant use. In particular, tulip tree, *Liriodendron tulipifera* (Magnoliaceae), the preferred host of *P. glaucus*, is toxic to *P. canadensis* larvae, while quaking aspen, *Populus tremuloides* (Salicaceae), the preferred host of *P. canadensis*, is toxic to *P. glaucus*. For each species, antennal sensitivity was measured by recording EAG responses to plant extracts of four hosts and one non-host of *P. glaucus*, which included tulip tree and quaking aspen.

MATERIALS AND METHODS

Insect source. Butterflies used in EAG studies were reared from eggs laid by wild-caught females on their natural host plants. *P. canadensis* females were collected from the first flight in the Battenkill River Valley area at the New York/Vermont border, U.S.A. and the larvae were reared to pupae in the field on sleeved tree branches of black cherry, *Prunus serotina* (Rosaceae). *P. glaucus* females were collected in Lancaster Co. in southeastern Pennsylvania, U.S.A. and were also field-reared on black cherry. After eclosion, butterflies were fed a honey-water solution and stored at 4° C for a maximum of 6 days until they were tested. By using adults that had not encountered any hosts prior to our assays and were reared on the same common host we prevented any influence due to adult or larval induction of preference (reviewed in Mercader & Scriber 2005).

Plant extracts. Leaves of tulip tree, L. *tulipifera* (Magnoliaceae), quaking aspen, *P. tremuloides* (Salicaceae), hop tree, *Ptelea trifoliata* (Rutaceae), sassafras, *Sassafras albidum* (Lauraceae), and spicebush, *Lindera benzoin* (Lauraceae) were collected from trees growing in Ingham Co. Michigan, U.S.A. in areas known to be pesticide free. For simplicity, hereafter hosts will be referred to by their common names. The detailed protocol for preparing plant extracts was described by Gökçe *et al.* (2005). In brief, dried and ground plant materials (10 g samples) were treated with 100 ml of methanol for 24 h. Thereafter, the suspensions were filtered through two layers of cheesecloth and the resulting extracts were stored until use in glass containers wrapped in aluminum foil in the dark at 4° C.

Electroantennograms (EAGs). The EAG apparatus and test protocols were a slight modification of those described in detail by Stelinski *et al.* (2003). The odor stimuli used were the plant extracts described above, methanol as a negative control, and hexanal (Aldrich Chemical Co., Milwaukee, WI, U.S.A., > 98 % pure) dissolved in hexane (Aldrich) as a positive control. Hexanal was used as a standard positive control given that synthetic green leaf volatiles are known to elicit EAG responses in *Papilio* species (Bauer & Feeny 1995). Two milligrams of each plant extract, hexanal solution, and methanol or hexane solvents alone (20 µL total solution) were pipetted onto 1.4 × 0.5 cm strips of Whatman No. 1 filter paper. These were aged for 5 min in a fume hood to allow for solvent evaporation. Subsequently, strips treated with extract or volatile treatments were inserted into glass Pasteur pipettes. EAG measurements were recorded as the maximum amplitude of depolarization elicited by 1 mL puffs of air through EAG-cartridges directed over antennae of live butterfly preparations. The time interval to expel 1 mL of stimulus odor or clean air was ca. 120 ms (Stelinski *et al.* 2003). Plant-extract or chemical stimuli were delivered through one arm of a glass Y-tube (each arm 2 cm in length, base 1 cm long, and 0.5 cm diameter) positioned approximately 5 mm from the antenna as carbon-filtered and humidified air was delivered at 50 mL/min into the second arm and onto the preparation via Tygon tubing.

Male and female butterflies of each species and sex were 2–6 d post-eclosion when used for EAG assays. Butterflies were mounted on 5.0 cm diameter plastic Petri dishes with a clay strip (30 × 5 mm) placed over their wings and thorax. EAG recordings were conducted by removing the terminal tip of the club (< 0.5 mm) of the antenna used for recording with fine scissors, and the recording electrode was positioned directly over the severed end. The reference electrode was inserted into the head near the base of the antenna. EAGs were performed ca. 30 s following mounting of butterflies and terminated at most 2 min later. For each plant extract

tested, EAGs were recorded from 8–10 insects of each sex and species. Plant-extract stimulations were presented to individual butterflies in random order, and control stimulations (filter paper impregnated with 20 µL of hexane or methanol) were delivered prior to each plant-extract stimulus presentation.

Statistical analyses. Between-species, pairwise comparisons of EAG responses were performed separately for tulip tree and quaking aspen on female responses using Mann-Whitney U tests with a Bonferroni corrected significance level of $\alpha < 0.05$. Within species, EAG responses for *P. canadensis* were log transformed and *P. glaucus* responses were square-root transformed to normalize the distributions and homogenize variance. Data were analyzed as repeated measures analysis of variance with individual butterfly as the subject, using Proc Mixed in the SAS System (SAS Institute 2000). The model included odor stimulus and sex as explanatory variables. Pair mean separations were performed for *P. canadensis* and *P. glaucus* using Tukey's multiple comparisons test.

RESULTS

EAG between species comparisons. There were significant differences between EAG responses of *P. canadensis* ($\chi^2 = 15.6$, df = 2, $P < 0.001$) and *P. glaucus* ($\chi^2 = 11.3$, df = 2, $P = 0.003$) to the extracts of tulip tree and quaking aspen (Fig. 1). The magnitude of EAG responses of *P. glaucus* was significantly greater to extracts of tulip tree than those of *P. canadensis*. In contrast, the magnitude of EAGs elicited by quaking aspen extracts was significantly higher for *P. canadensis* than *P. glaucus*.

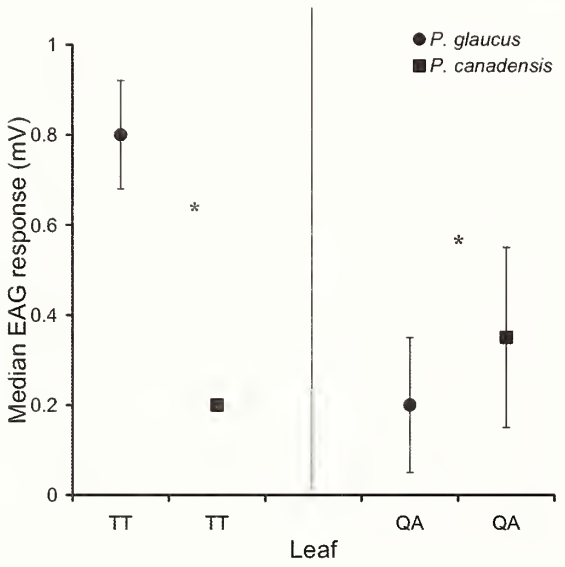

Fig. 1. Median EAG responses of *P. glaucus* and *P. canadensis* females to the extracts of tulip tree TT (*Liriodendron tulipifera*) and quaking aspen QA (*Populus tremuloides*). Bars around the medians represent the inter-quartile ranges (*P. canadensis* inter-quartile range for tulip tree is smaller than size of square). Pair-wise differences were analyzed for each extract using the Mann-Whitney U tests. Values within extract with an * had a significant difference at Bonferroni corrected $\alpha < 0.05$.

EAG within species comparisons. Within-species odor stimuli had a significant effect for *P. glaucus* ($F = 50.1$, df=6,102, $P < 0.0001$), and *P. canadensis* ($F = 24.67$, df = 6,108, $P < 0.0001$). There was no significant sex-by-odor stimulus interaction for *P. glaucus* or *P. canadensis*; therefore, male and female responses were combined for analysis of pair-wise differences (Tables 1

Table 1. Mean EAG responses ± SE of male and female *P. glaucus*. Data for males and females were combined for analysis given that there was no significant sex by odor stimulus interaction.

	Mean ± SE EAG antennal response (mV) to plant extracts				
Odor sources	Males	N	Females	N	P < 0.05
Methanol	0.07 ± 0.01	8	0.09 ± 0.02	10	c*
Hexanal	0.70 ± 0.06	8	0.60 ± 0.09	10	a
Tulip Tree	0.85 ± 0.07	8	0.87 ± 0.07	10	a
Quaking Aspen	0.26 ± 0.07	8	0.19 ± 0.04	10	b
Sassafras	0.23 ± 0.05	8	0.22 ± 0.04	10	b
Spicebush	0.23 ± 0.04	8	0.30 ± 0.04	10	b
Hop Tree	0.25 ± 0.04	8	0.28 ± 0.07	10	b

*Significant differences in antennal responses to odorant stimuli are indicated by different lowercase letters ($P < 0.05$, Tukey's HSD).

Table 2. Mean EAG responses ± SE of male and female *P. canadensis*. Data for males and females were combined for analysis given that there was no significant sex by odor stimulus interaction.

	Mean ± SE EAG antennal response (mV) to plant extracts				
Odor sources	Males	N	Females	N	P < 0.05
Methanol	0.14 ± 0.03	10	0.09 ± 0.02	9	d*
Hexanal	0.57 ± 0.07	10	0.60 ± 0.09	9	a
Tulip Tree	0.21 ± 0.03	10	0.24 ± 0.03	9	c
Quaking Aspen	0.43 ± 0.07	10	0.37 ± 0.05	9	a
Sassafras	0.30 ± 0.06	10	0.46 ± 0.09	9	abc
Spicebush	0.35 ± 0.05	10	0.41 ± 0.04	9	ab
Hop Tree	0.28 ± 0.05	10	0.29 ± 0.06	9	bc

*Significant differences in antennal responses to odorant stimuli are indicated by different lowercase letters ($P < 0.05$, Tukey's HSD).

and 2). *P. glaucus* exhibited higher EAG responses to its preferred host, tulip tree, than to less-preferred hosts, hop tree, sassafras, and spicebush, and the non-host quaking aspen (Table 1). Responses to tulip tree were similar to those elicited by the hexanal positive control (Table 1). Likewise, *P. canadensis* exhibited a significantly higher EAG response to its preferred host, quaking aspen, than to hop tree or tulip tree (Table 2). Once again, responses to the preferred host were not different from those elicited by the synthetic standard (Table 2). However, EAGs elicited by two of the non-hosts, sassafras and spicebush, were not significantly different from those elicited by quaking aspen for *P. canadensis*. There was no difference between responses to methanol versus hexane solvents alone; hence, data are not shown for the latter negative control.

DISCUSSION

Antennal sensitivity of *P. glaucus* was approximately three-fold higher to extracts of the preferred host, tulip tree, than to any other extract tested (Table 1). Conversely, tulip tree extract elicited a weaker antennal response from *P. canadensis* than the others tested (Table 2). Furthermore, EAGs recorded from *P. canadensis* to extracts of this species' preferred host plant, quaking aspen, were greater than those from *P. glaucus* (Fig. 1). These results agree with the prediction that peripheral sensitivity to primary hosts should be greater than to less preferred hosts in generalist butterfly species if olfactory cues play a role in host finding behavior. It is notable that species-specific responses were recorded to preferred host plants despite the use of extracts of dried leaves in the current study, which may have limited our assay to higher molecular weight volatiles. This suggests that these butterfly species may use host-plant volatiles, at least as short-range cues, while foraging for suitable host plants, which agrees with field observations of *P. glaucus* females hovering, but not landing, on non-hosts while searching for oviposition sites (R. J. M. personal observations).

Although *P. glaucus* is a highly polyphagous swallowtail species, females exhibit a distinct ovipositional preference for tulip tree throughout their range (Scriber *et al.* 1991; Mercader & Scriber 2005), even in populations where this host plant does not occur (Bossart & Scriber 1995). Congruently, antennal responses to tulip tree were approximately three times greater than to another major host (hop tree), two secondary hosts (sassafras and spicebush), and a non-host (quaking aspen). Although the EAG technique cannot distinguish between attractive versus deterrent olfactory stimuli, the heightened antennal sensitivities recorded in this study corresponded well with known host plant preferences of both species.

It is important to note that although greater EAG responses were observed for females of *P. canadensis* for its most common host quaking aspen than all other hosts tested, these were not significantly different than those for the marginal host sassafras and non-host spicebush (Table 2). This lower specificity in *P. canadensis* relative to *P. glaucus* is not unique to the olfactory system. In ovipositional arenas that primarily test contact chemoreception, *P. canadensis* females have a significantly lower specificity than *P. glaucus*, including a high acceptance rate for the non-host tulip tree (Scriber *et al.* 1991; Mercader & Scriber 2007). This lower specificity in *P. canadensis* is likely to be due to the absence of plants in the Lauraceae (e.g. sassafras and spicebush), Magnoliaceae (e.g. tulip tree), and Rutaceae (e.g. hop tree) where *P. canadensis* occurs, greatly reducing the selection pressure for higher specificity.

Interestingly the divergence in antennal sensitivity between *P. glaucus* and *P. canadensis* was observed in both males and females (Tables 1 and 2). As males do not oviposit and these species do not mate on host plants, divergence in sensitivity to host plant odors does not have any clear advantage for the males of these two species. This similarity in the antennal sensitivities of males and females in both species may reflect a developmental similarity between males and females (with no adaptive function in males) or serve an unknown function.

Heightened antennal sensitivity of *P. glaucus* to tulip tree relative to the other host extracts tested lends support to the hypothesis that olfactory cues may be used to reduce decision-making time during host-plant selection in this species. Pre-alighting cues are more likely involved in maximizing rates of oviposition than in host acceptance behavior (Thompson & Pellmyr 1991); therefore, it is likely that olfactory cues may be used to maximize *P. glaucus*' rate of landing on tulip tree wherever this preferred host is present. Furthermore, the higher sensitivity of *P. canadensis* to odors of quaking aspen relative to the other less-preferred plant species evaluated here adds further support to the hypothesis that host-plant location may be, in part, mediated by chemical signals in these two generalist, sister butterfly species. Further laboratory and field behavioral assays will need to be conducted to confirm this hypothesis.

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DESCRIPTION OF THE IMMATURE STAGES OF *METHONA CONFUSA CONFUSA* BUTLER, 1873 AND *METHONA CURVIFASCIA* WEYMER, 1883 (NYMPHALIDAE, ITHOMIINAE) FROM EASTERN ECUADOR

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ABSTRACT. Here we describe the complete life history for *Methona confusa confusa* Butler, 1873 and *Methona curvifascia* Weymer, 1883 from eastern Ecuador. Each stage from egg to pupa is described and illustrated. Descriptions of first instar chaetotaxy and instar durations are also reported. Both species were found feeding on *Brunfelsia grandiflora schultesii* Plowman. Mature *M. confusa* larvae have 12 transverse bands that are all yellow in color, including one on segment A9 as observed for *M. megisto* and *M. themisto*. In contrast, *M. curvifascia* lacks a transverse band on segment A9, having 11 transverse bands in total that are white in middle segments and orange in anterior and posterior segments. The pupa of *M. confusa* and *M. curvifascia* differs in the arrangement of spots on the thorax dorsum.

Additional key words: *Brunfelsia grandiflora*, chaetotaxy, egg clustering, Solanaceae.

Butterflies in the genus *Methona* Doubleday, 1847 (Ithomiinae) are large, warningly colored butterflies illustrated in the original descriptions of both Batesian (*M. confusa*) and Müllerian (*M. megisto*) mimicry (Bates 1862; Müller 1879). Despite being involved in the conception of a theory that has generated a massive publication record, *Methona* biology is relatively poorly understood. The genus *Methona* is distributed across much of South America east of the Andes reaching its southern limit in southern Brazil, extreme northern Argentina and Uruguay (Forbes 1943; Mielke & Brown 1979; G. Lamas pers. comm.). In addition, Lamas (2004) indicates that two new subspecies of *M. confusa* are present in Panama.

Host records have been published for four of the seven recognized species and *Methona* are apparently monophagous on the Solanaceae genus *Brunfelsia* (Brown 1987; Drummond 1976, 1986; Drummond & Brown 1987). However, only three species have any published information on immature stage morphology (Brown 1987; Brown & Freitas 1994; Drummond 1976; Motta 2003; Willmott & Freitas 2006), and a complete description of the immature stages has not been published for any species in the genus. Here we report on the immature stages of two species of *Methona* from the upper Amazon basin in eastern Ecuador, *Methona confusa confusa* Butler, 1873 and *M. curvifascia* Weymer, 1883. Both of these species are residents of the Amazon basin, however *M. confusa* is distributed more broadly, occurring throughout the whole basin (and including the populations in Panama mentioned above), and *M. curvifascia* is restricted to western Amazonia (G. Lamas pers. comm.). We describe all early stages, report instar durations and provide detailed description of first instar chaetotaxy and briefly discuss differences in larval color pattern in the genus.

Materials and Methods

Observations were made from January to February 2007 in Provincia Sucumbios, Ecuador, in the forests surrounding Garzacocha (00°29.87'S, 76°22.45'W) and Challuacocha (00°26.29'S, 76°16.81'W). Early stages were reared in plastic cups and plastic bags under ambient conditions (22–30° C, 70–100% relative humidity) in a wood building with screen windows. Larvae were moved daily to a shaded environment under a nearby building to maintain ambient conditions. Observations were recorded daily and head capsules and pupal exuviae were collected. Larval specimens were boiled and subsequently stored and studied in 70% ethanol. Vouchers are deposited in the Essig Museum of Entomology at UC Berkeley. Descriptions other than first instar chaetotaxy are based on several individuals from a single clutch of eggs for *M. confusa*, and more than 10 individuals for *M. curvifascia*. First instar chaetotaxy follows nomenclature of Motta (2003), and Hinton (1946), Kitching (1984) and Peterson (1962) were also consulted. The number of specimens for which first instar chaetotaxy was examined is listed in Appendix 1. Host plant vouchers are deposited in the University and Jepson Herbaria at UC Berkeley (voucher number RIH-1424, UC accession #

UC1933451) and Herbario Nacional de Ecuador (voucher number RH01-117).

RESULTS

Methona confusa confusa Butler, 1873

Hostplant. *Brunfelsia grandiflora schultesii* Plowman (Solanaceae), known locally as chiricaspi. The group of *M. confusa* eggs was found on an individual plant that also hosted eggs of *M. curvifascia*.

Oviposition. Not observed. Eggs occur in large clusters on the underside of fresh but mature sized leaves. One cluster of 46 unhatched eggs (at 1.5 m) and a cluster of 18 hatched eggs were found. Plants with eggs were ~2m tall and located in shaded areas at gap edges.

Egg. Figure 1A. Duration: Unknown. Eggs hatched four days after found in the field. Egg is white, adorned with 9–11 horizontal and 19–22 vertical ridges making many small rounded cells. Mean egg height = 1.23 mm (s.d. = 0.04, n = 3). Mean egg width = 0.98 mm (s.d. 0.03, n = 3). Mean axes ratio (height/width) = 1.26 (s.d. = 0.01, n = 3).

1st instar. Figure 1B & C. Duration: 3 to 7 days. Mean head capsule width = 0.77 mm (s.d. = 0.02, n = 10). Head capsule and thoracic legs are black. Proleg shields are large and black. Anal plate is present and shiny black. Body is covered with short pale setae. Body is widest near the head and tapering posteriorly. Body is dark olive green with paler olive transverse bands. Body has pale transverse bands with slightly raised ridges within, ridge on A1 & A2 most pronounced. Larvae eat channels into the leaf from the margin consuming all layers of the leaf.

See Appendix 1 for description of first instar chaetotaxy. An additional lateral body seta (Figure 2) was observed on the meso- and metathorax of the two larvae studied compared with the ithomiines studied by Motta (2003), including *Methona themisto*. This seta is assigned to the lateral group in descriptions (Appendix 1) because this keeps other setae consistent with adjacent segments and the lateral group has a third seta in some moth families (Hinton 1946). Thus, the top seta is inferred to be L1 with the middle L2 and most ventral L3 (Fig. 2). Descriptions of characters involving setae L1 and L2 on these segments should be treated with caution, as homology of L1 and L2 may not have been correctly inferred.

2nd instar. Figure 1D. Duration: 4 to 6 days. Mean head capsule width = 1.18 mm (s.d. = 0.04, n = 10). Like the previous instar with the following observations: body is brown and transverse bands are dirty white with tints of yellow. Segments T1-A9 have a transverse band making 12 bands total. The transverse band on segments A3-A6 leans slightly to the posterior. The transverse pale band is located in the posterior of each segment except T1, which is pale anteriorly and almost entirely pale. Transverse ridges are more pronounced this instar.

3rd instar. Figure 1E. Duration: 3 to 4 days. Mean head capsule width = 1.69 mm (s.d. = 0.04, n = 5). Like previous instar with the following observations: body a rich dark brown and transverse bands dirty white first day turning yellow subsequently. Rest on underside of leaf, sometimes with body straight, sometimes curled in a "J" (Fig. 1I1).

4th instar. Figure 1F. Duration: 4 to 7 days. Mean head capsule width = 2.50 mm (s.d. = 0.07, n = 5). Like previous instar with the following observations: transverse bands are yellow and slanting slightly toward the posterior. Transverse bands on A3–6 extend farthest ventrally and are not as pointed at their terminus. Transverse band on A9 is smaller than others, extending the shortest distance ventrally. Laterally, rounded protuberances form a fleshy shelf. Transverse ridges run across this shelf ending below it. The transverse ridges are generally located in the anterior of the transverse yellow band on each segment. Spiracle on T1 is located at posterior margin of yellow band, all other spiracles are anterior of yellow band. Body is covered in short pale pubescence.

5th instar. Figure 1G & H. Duration: 8 to 12 days. Mean head capsule width = 3.39 mm (s.d. = 0.20, n = 4). Like previous instar with the following changes and observations: body dark brown, appearing black in some individuals, with yellow transverse bands. Area of yellow transverse band posterior to ridge fades to whitish on segments A3–6. Yellow bands fade slightly laterally. The day before pupating the yellow fades in all bands.

Pupa. Figure 1I, J & K. Duration: 12 days. Pupa is pendant and bent near abdomen tip but not at abdomen-thorax junction. Pupa colored yellow with distinct black marks. Dorsally with two rows of thin black marks that are thinnest near head. Last segment before cremaster has these dorsal marks merged into wide line. Cremaster is black. Spiracles are outlined in thick black marks. Wing pad has costal margin marked with black. Wing pad posterior margin along thorax marked with black that breaks up into dots near spiracles. Center of wing pad has broken black lines. Ventrally is an inverted black mushroom-shaped spot anterior of cremaster that surrounds a pair of black tubercles. Ventrally at edge of wing pad two black marks merge together. Ocular caps marked with black that starts near eye and extends ventrally as a thick line. Ventrally central black marks over legs and black marks near base of antennae. Thorax slightly keeled with three black marks: anterior spot elongate and thickest toward head, middle one elongate and forked, and posterior one an elongate spot that is widest in the middle (Fig. 1J). The extent of dark markings is variable with some individuals with heavier dark markings (Fig. 1J).

Eyes darken one to two days before eclosing. The day before eclosing black and gold appear in wing pad, then wing pad turns black, followed by abdomen. Pupa has unpleasant odor, as does freshly eclosed adult.

Methona curvifascia Weymer, 1883

Hostplant. *Brunfelsia grandiflora schultesii* Plowman (Solanaceae).

Oviposition. A female was observed ovipositing on a relatively small host from 11:30–12:30. The plant was 1.25–1.5 m tall and located in tall secondary growth with bright light but shaded by a thin canopy of leaves. The female flew to host leaves, tapped the upper surface of the leaf, and then would land on these leaves, occasionally opening her wings and antennating the leaf. She did this repeatedly for 40 minutes. She then landed on a leaf at 0.5 m and hung at its edge, curled her abdomen under and laid a single egg on the underside of the leaf. She was obscured from view after laying this egg but remained close to the site where she laid for ~ 3 min. She then flew to a nearby bird dropping and fed from it. Three eggs were found where she laid the one observed, so she may have laid all three in a few minutes although only the one was observed. Two other eggs were found on this plant along with a freshly hatched first instar. Egg placement with respect to the leaf border appeared somewhat variable and not confined to the leaf border, with eggs sometimes being closer to the leaf midvein than leaf border. Leaves chosen for oviposition varied from small younger growth (3–5 cm in length) to fresh nearly full-sized leaves (8–10 cm). Other plants hosting eggs/larvae were ~2 m tall and found in shaded areas at the edge of primary forest gaps.

Egg. Figure 3A. Duration: 6 days (n = 1). Mean egg height = 2.05 mm (s.d = 0.10, n = 3). Mean egg width = 1.30 mm (s.d. = 0.05, n = 3). Mean axes ratio (height/width) = 1.58 (s.d. = 0.07, n = 3). Egg is white, widest two-thirds the distance from base but only slightly wider there. Egg adorned with 14–17 horizontal and 26–30 vertical ridges. The horizontal and vertical ridges make rounded cells that merge near the apex. Head capsule is visible at egg apex one day before hatching.

1st instar. Figure 3B. Duration: 3 days (n = 2) to 4 days (n = 2). Mean head capsule width = 0.90 mm (s.d. = 0.03, n = 2). When first hatched body is dark grey with paler grey transverse bands in anterior of T1 and posterior of segments T2–A8 making 11 pale bands in total. Within each pale band is a raised transverse ridge that crosses the dorsum. Body covered in short pale setae. Head capsule black and thoracic legs are black. Proleg shields large and black. Black sclerotized anal plate present. Second day and beyond, body dark brown with white to dirty white transverse bands (Fig. 3B). Transverse bands widest dorsally, more narrow laterally. Transverse band on T1

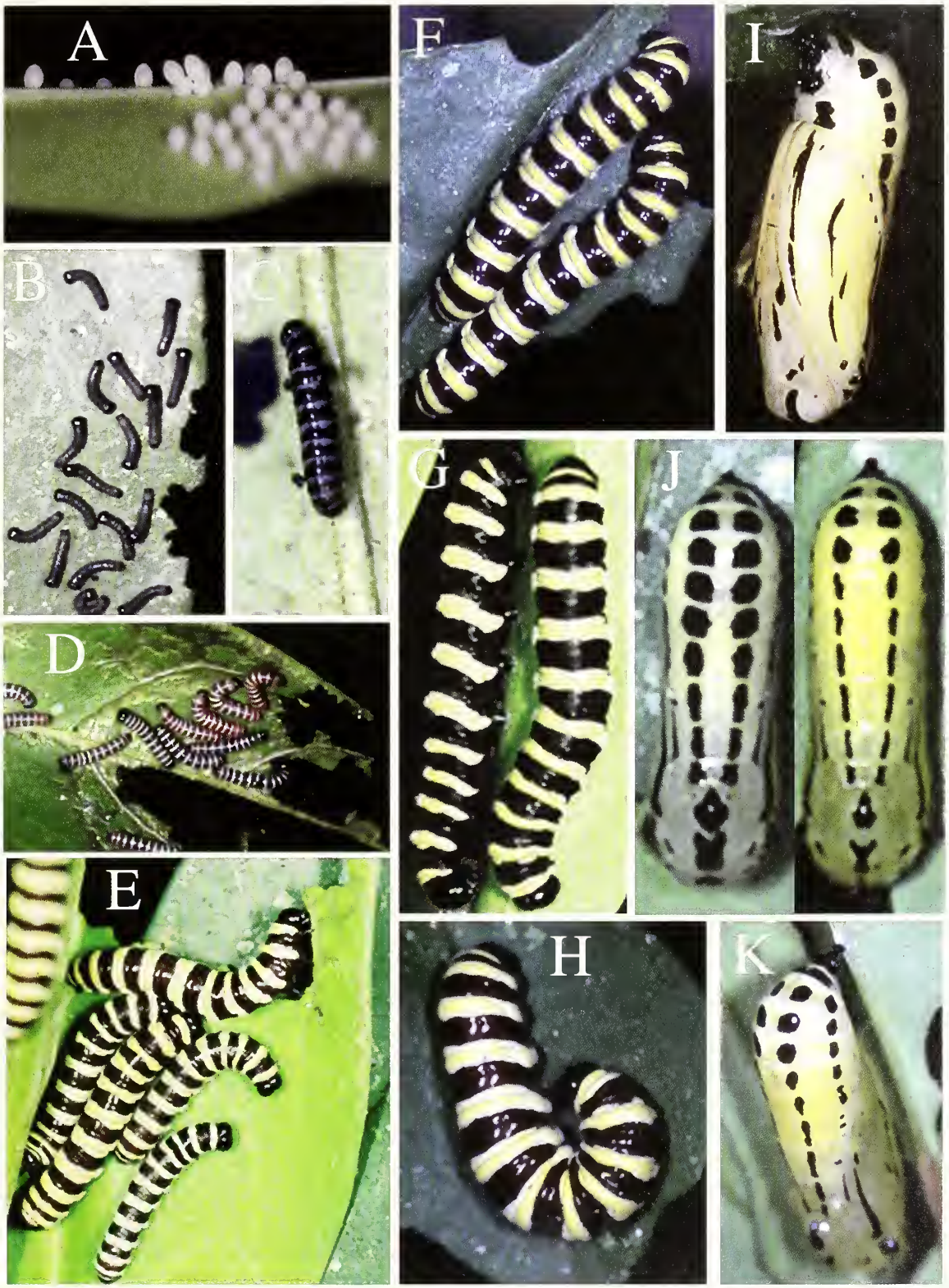

FIG. 1. *Methona confusa* immature stages. A. Egg clutch. B. First instar, first day with very pale bands, feeding from leaf margin. C. First instar > 1 d old with pale bands. D. Second instars, midmolt first instars and feeding damage. E. Third instar. F. Fourth instar. G. Fifth instar. H. Fifth instar in resting position. I. Ventro-lateral view of pupa. J. Dorsal view of two pupae showing range of variation in black markings. K. Dorso-lateral view of pupa illustrating detail near cremaster.

wider than other segments dorsally. Larvae eat little, to more than three quarters egg when first hatched. Larvae feed at leaf margin making channels into side of leaf (Fig. 3C & D). See Appendix 1 for description of first instar chaetotaxy.

2nd instar. Figure 3C. Duration: 3 days (n = 2) to 4 days (n = 1). Mean head capsule width = 1.33 mm (s.d. = 0.03, n = 4). Like previous instar with the following observations: First day, white transverse band of T1 and T2 now with yellow tints. Second day and beyond, transverse band on T1 is yellow and white transverse band on T2 and A8 with yellow tints. Raised ridges more pronounced this instar, with T1 less pronounced than other segments. On segments A3–6 the transverse white band bends forward laterally and ends just above the proleg. Spiracles dark. Spiracle on T1 surrounded by yellow in posterior of transverse band. Spiracles in other segments located at anterior margin of bands.

3rd instar. Figure 3D. Duration: 3 days (n = 6) to 4 days (n = 1). Mean head capsule width = 2.00 mm (s.d. = 0.15, n = 8). Like previous instar with the following observations: Body is very dark brown, some individuals appearing matte black. Non-white bands are more orange-yellow this instar. First day, transverse band on T2 and A8 more strongly colored than previous instar, and orange-yellow like T1, band on T3–A7 white. Second day and beyond, transverse band on segments T3, A1 (only some individuals), and A7 develops yellow tints. Transverse bands extend farthest toward venter on segments A3–6.

4th instar. Figure 3H. Duration: 5 days (n = 3), 6 days (n = 2), 7 days (n = 2). Mean head capsule width = 2.70 mm (s.d. = 0.06, n = 12). Like previous instar with the following observations: Transverse band on T1, T2 and A8 is orange and band on segments T3, A1, A2 and A7 is tinted orange this instar. Transverse band on A7 is wider than other bands except for that on T1.

5th instar. Figure 3I. Duration: 9 days (n = 1), 11 days (n = 7), 12 days (n = 4), 13 days (n = 1). Mean head capsule width = 3.70 mm (s.d. = 0.19, n = 6). Like previous instar with the following observations: Head capsule narrows dorsally with two subtle humps and has short dark setae. Clypeus area is pale grey and frontal sutures pale colored. Body is very dark brown appearing matte black in some individuals. Thorax has additional wrinkles between ridges dorsally. Pale body pubescence more pronounced on ridges. Transverse band on T1 & 2 is orange turning white just above leg where it ends without tapering. Transverse band on segment T3 is white, tinted with orange dorsally and ends above leg without tapering. Transverse band on A1 & A2 tinted orange dorsally, and is white where terminates ventro-laterally in narrow point (A1 narrower point than A2). Segments A3–6 with white transverse band that bends slightly to posterior just before terminating on fleshy bulge above proleg. A7 with white band tinted orange and terminating in rounded point ventro-laterally. A8 band is orange, but not as bright as T1 & T2, and turns white before tapering to a point ventro-laterally. Orange coloration becomes more extensive and white bands on A3–6 darken two to three days before pupating.

Larvae in all instars rest on underside of leaf with head down near where feeding. Larvae tend to feed first at distal end of leaf and subsequently toward leaf base in later instars. Larvae raise thorax off substrate or curl into tight "J" when disturbed.

Pupa. Figure 3E, F, G & J. Duration: 11 days (n = 4) to 12 days (n = 1). Pupa is pendant and bent near abdomen tip but not at abdomen-thorax junction. Pupa is yellow and marked with distinct black spots. Black marks develop within a couple hours of pupating. Head and thorax are slightly darker yellow than abdomen and wing pad. Abdomen dorsum with two rows of black marks that become larger and more rounded toward abdomen apex, and merge into thick line on A10. Laterally, abdomen has seven black spots over spiracles that increase in size toward abdomen apex. Lateral abdomen marks not in a straight line, with marks on A3 & A4 at wing pad margin out of line with the others. Wing pad has three black lines near its center, black spots along its dorsal margin that become lines basally, and black lines along its ventral margin. Ocular caps colored black, with black extending into a line ventrally. Black cremaster. Thorax dorsum has a pair of anterior black spots, a single medial spot near the anterior pair and another spot posteriorly. Venter has rough upside down "T" near the cremaster that surrounds two black tubercles. Some variation observed in extent of dark spots on the thorax (Fig. 3E & F).

Eyes become dark one to two days before eclosion, followed by black and yellow visible in wing pad. Pupa becomes nearly black just before eclosing.

DISCUSSION

Our observations provide several early stage characters useful for distinguishing *Methona confusa* and *M. curvifascia* at this site. Larval coloration differs between these two species with *M. confusa* exhibiting 12 transverse bands similarly yellow in color along the body, whereas *M. curvifascia* has 11 bands with those in the middle of the body white, and those at either end orange. The pupa of these two species can be distinguished by the black spots on the thorax dorsum. *M. confusa*'s anterior spot consists of a single spot and its middle spot is "Y" shaped, whereas *M. curvifascia*'s anterior spot is split into two small spots and its middle spot is round. Observed variation in the extent of black markings on the pupa is illustrated in Fig. 1J and Fig. 3E&F and does not appear to pose problems for identification using the aforementioned pupal characters. *M. confusa* eggs are laid in clusters and are shorter (p = 0.002, t = 13.1, n =3, see above descriptions for means) and narrower (p = 0.001, t = 10.7, n =3, see above descriptions for means) than *M. curvifascia*. *M. confusa* eggs are also relatively more rounded with a lower axes ratio than *M. curvifascia* (p = 0.013, t = 8.2, n = 3, see above descriptions for means).

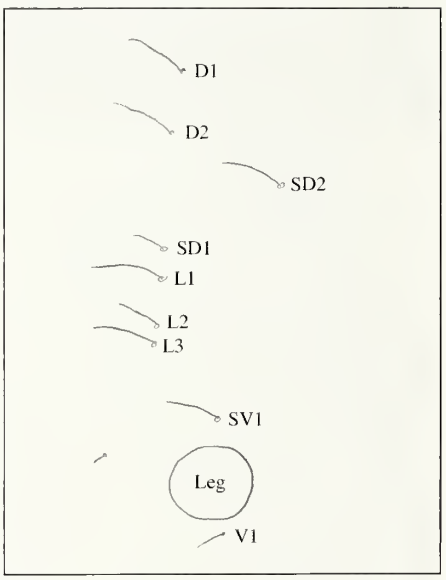

FIG. 2. Schematic of *Methona confusa* first instar chaetotaxy for meso- and metathoracic segments illustrating additional lateral seta (L3). Arrangement of body setae on other segments for *M. confusa* otherwise resembles *M. themisto* (Figure 19.3 in Motta 2003) except for characters 92 and 93 which are described in Appendix 1.

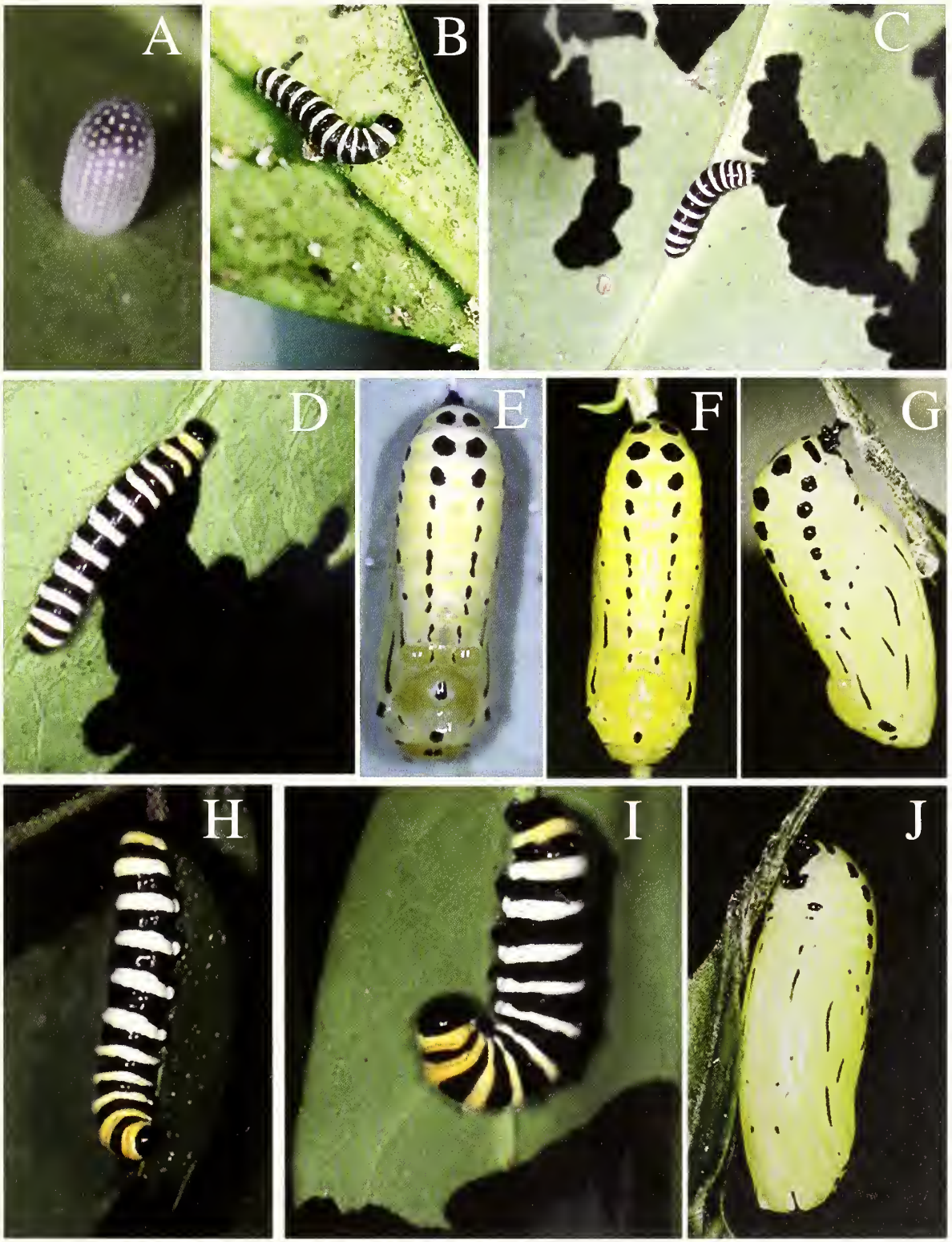

FIG. 3. *Methona curvifascia* immature stages. A. Egg. B. First instar. C. Second instar on leaf showing feeding damage of young instars. D. Third instar. E. Dorsal view of freshly formed (< 1 d) pupa. F. Dorsal view of pupa exhibiting mature coloration. Note variation in black mark on thorax. G. Lateral view of pupa. H. Fourth instar showing feeding position and damage. I. Fifth instar showing resting behavior. J. Ventral view of pupa.

Observations made here also allow comparison of larval morphology within and among *Methona* species. The *M. confusa confusa* larvae observed here are similar to the *M. confusa psamathe* larva figured in Brown (1987). Although it is difficult to see, the larva in Brown (1987) Figure 8X appears to have a transverse band on segment A9 making 12 transverse bands in total. The presence of a transverse band on A9 in *M. confusa* is a trait shared with *M. megisto* and *M. themisto* illustrated in Brown & Freitas (1994) and was identified as a synapomorphy of *Methona* in Willmott & Freitas (2006)(Table 2, character 49:1). However, *M. curvifascia* lacks the transverse band on A9 indicating that not all *Methona* have this character. *M. curvifascia* is placed as the basal *Methona* species in a molecular phylogenetic study (Hill unpublished) suggesting that absence of a transverse band on A9 is the plesiomorphic condition, and evolution of the extra band on A9 occurred after *M. curvifascia* diverged from the rest of the group. *Methona curvifascia* also may be divergent in egg shape with a mean axes ratio observed here just outside of the range indicated for *M. themisto* (Brown & Freitas 1994) and significantly different than *M. confusa* as mentioned above.

Aside from the characters just discussed, observations made here are congruent with most of the synapomorphies for *Methona* larvae listed in Table 2 of Willmott & Freitas (2006). The pupa of both *M. confusa* and *M. curvifascia* exhibit the sharp curve along the dorsum in the posterior half of the abdomen (character 55:1). The following characters, with their states indicated in parentheses, are also the same for *M. confusa* and *M. curvifascia* as listed for *M. megisto* and *M. themisto* in Willmott & Freitas (2006): 22(1), 54(0), 56(0), 59(1).

Willmott & Freitas (2006) report that *M. megisto* and *M. themisto* lay eggs at the border of leaves and this is indicated as a synapomorphy for the genus (table 2, character 9:1), however observations on egg placement for both *Methona* species reported here seem to conflict with this character state. *M. confusa* lay eggs in clusters that covered a large portion of the leaf, including the middle of the leaf (Fig. 1), although scoring this species for this character seems inappropriate because of its cluster-laying habit. It is likely that *M. confusa* lays eggs while resting on the topside of the leaf, but given its cluster laying behavior it would be interesting to confirm this. *M. curvifascia* oviposition location does not seem confined to the leaf border, although this may be a result of relatively small host leaf size observed here, because on hosts with larger leaves, laying from the leaf top and curling the abdomen underneath would result in eggs placed near the border. Thus, it may be useful to re-evaluate this character by focusing more on female oviposition behavior and less on the resulting egg position.

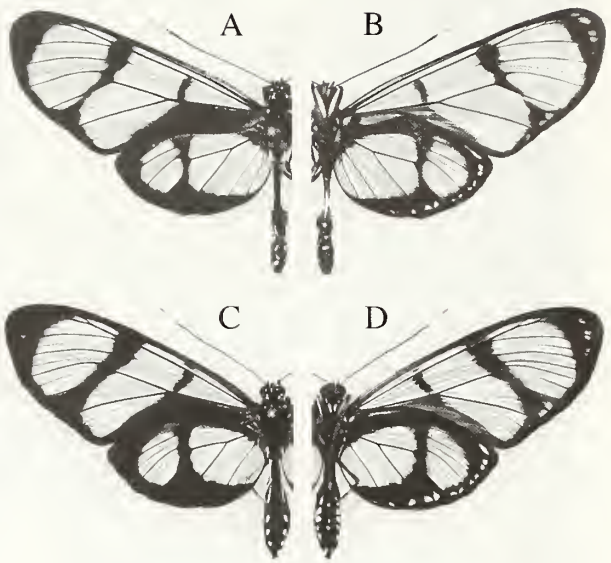

FIG. 4. Adult *Methona* reared in this study. A. Male *M. confusa dorsum*. B. Male *M. confusa* venter. C. Female *M. curvifascia* dorsum. D. Female *M. curvifascia* venter. *M. confusa* were identified by vein Sc coalescing with R1, presence of dorsal hindwing costal "hair pencils" in females, and male last abdominal tergite not produced and block-like or spine-like. *M. curvifascia* were identified by vein Sc not coalescing with R1, absence of dorsal hindwing costal "hair pencils" in females and male last abdominal tergite produced and narrowing into a spine-like process.

Methona confusa is the first species in the genus to be observed laying eggs in clusters. In addition to the observation here, A. Freitas observed a female *Methona* in Acre, Brazil laying a cluster of 12 eggs. The female escaped after ovipositing but was likely *M. confusa* (A. Freitas, pers. comm.). Cluster-laying has been found to be relatively rare in ithomiines, but it is widely distributed across their phylogeny, being present in 12 genera (including *Methona*) (Brown & Freitas 1994; Drummond 1976; Haber 1978; Hill 2006; Willmott & Freitas 2006). Indeed, using the tribal classification of Willmott & Freitas (2006), only the tribes Tithoreini and Oleriini lack any cluster-laying species. In addition to *Methona*, the genera *Hypothyris, Episcada, Ithomia*, and *Pteronymia* contain cluster-laying species as well as species known to lay eggs singly (Brown & Freitas 1994; Willmott & Freitas 2006; Hill pers. obs.). This suggests life history studies on additional ithomiine species could reveal cluster-laying species in other genera presently known to only lay solitary eggs.

Some ithomiine species that are documented laying eggs in clusters also exist in solitary-laying populations, and this may be the case with *M. confusa* as well. In contrast to the *M. confusa* immatures studied here, Brown (1987) illustrated a single *M. confusa* larva from Venezuela suggesting it was solitary. Of course, Brown's (1987) larva could have been part of a cluster of eggs that had dispersed at some larval stage only appearing to be more or less solitary. Larvae studied here were confined to bags and so no observations on dispersal of a larval group were made. It would be interesting to confirm whether *M. confusa* populations vary in cluster-laying because this would be an additional example of intraspecific variation similar to what has been observed in two other ithomiine species. Gilbert (1969) observed *Mechanitis menapis saturata* laying eggs in clusters in Costa Rica, but Drummond (1976) found *M. menapis mantinens* laying single eggs in western Ecuador. Similarly, Gilbert (1969) reported *Hypothyris euclea valora* (called *H. e. leucania*) laying eggs in clusters in Costa Rica, and Drummond (1976) observed *H. euclea intermedia* (called *H. e. peruviana*) laying single eggs at Limoncocha. In contrast to Drummond's (1976) observation we have observed *H. euclea intermedia* laying eggs in clusters at Garzacocha. Such intraspecific variation could be a fruitful area for investigating hypotheses for cluster-laying in ithomiines (Clark & Faeth 1998; Courtney 1984; Haber 1978; Stamp 1980; Vasconcellos-Neto 1986; Young & Moffett 1979), and indicates the continuing importance of immature stages to understanding ithomiine biology.

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Please see Appendix on next page

APPENDIX 1. First instar chaetotaxy of *Methona confusa* and *Methona curvifascia*. For the reasons given in Hill (2006), characters are listed as text here rather than as states of Motta's (2003) characters. No larval specimens of *M. curvifascia* were preserved for study of body chaetotaxy. Descriptions of body setae are based on two larvae for *M. confusa*. Descriptions of head, labrum and mandible chaetotaxy are based on two head capsules for *M. curvifascia* and five head capsules for *M. confusa*.

Character # of Motta	*M. confusa*	*M. curvifascia*
Head capsule		
1	Seta C1 equidistant to frontal and anteclypeal sutures	Seta C1 equidistant to frontal and anteclypeal sutures
2	Seta C2 nearer to C1 than to a medial imaginary line	Seta C2 nearer to C1 than to a medial imaginary line
3	Seta C2 same length at C1	Seta C2 same length at C1
4	Seta F1 undoubtedly more dorsal and medial to C2	Seta F1 undoubtedly more dorsal and medial to C2
5	Seta F1 nearer to C2 than it is to coronal bifurcation	Seta F1 nearer to C2 than it is to coronal bifurcation
6	Seta F1 subtly nearer to frontal suture than to imaginary medial line	Seta F1 subtly nearer to frontal suture than to imaginary medial line
7	Puncture Fa aligned with seta F1	Puncture Fa subtly above seta F1
8	Distance between Fa punctures subtly longer than distance between Fa and seta F1	Distance between Fa punctures similar to that between Fa and F1
9	Puncture AFa, and setae AF1 and AF2 all present	Puncture AFa, and setae AF1 and AF2 all present
10	Puncture AFa slightly medial of line connecting setae AF1 and AF2	Puncture AFa in line with to slightly medial of line connecting setae AF1 and AF2
11	Puncture AFa equidistant to setae AF1 and AF2 (or subtly nearer to AF1)	Puncture AFa equidistant to setae AF1 and AF2 (or subtly nearer to AF2)
12	Setae AF1 and AF2 similar in length	Setae AF1 and AF2 similar in length
13	Seta AF2 subtly above level of coronal suture bifurcation	Seta AF2 subtly above level of coronal suture bifurcation
14	Distance of seta AF2 to coronal suture same as distance of AF1 to frontal suture	Distance of seta AF2 to coronal suture same as distance of AF1 to frontal suture
15	Puncture Aa below imaginary line connecting AF1 and A2	Puncture Aa above imaginary line connecting AF1 and A2
16	Puncture Aa nearer to A2 than to AF1	Puncture Aa nearer to A2 than to AF1
17	Seta A3 posterior to imaginary line between stemma iv and P1; distance of A3 to the imaginary line less than distance of A3 to stemma iv	Seta A3 posterior to imaginary line between stemma iv and P1; distance of A3 to the imaginary line less than distance of A3 to stemma iv
18	Seta A1 slightly closer to stemma i than ii and aligned to slightly above stemma i	Seta A1 closer to stemma i than ii and aligned to slightly above stemma i
19	Seta A2 aligned with imaginary line between stemma ii and AF1	Seta A2 aligned with imaginary line between stemma ii and AF1
20	Seta A3 not much longer in length than A2 and L1	Seta A3 not much longer in length than A2 and L1
21	Puncture Pa ventral to slightly ventral to imaginary line connecting setae A2 and A3.	Puncture Pa ventral to slightly ventral to imaginary line connecting setae A2 and A3.
22	Puncture Pa nearer to seta A2 than to A3	Puncture Pa nearer to seta A2 than to A3
23	Puncture Pb aligned with, to slightly medial of, imaginary line between setae P1 and P2.	Puncture Pb aligned with, to medial of, imaginary line between setae P1 and P2.
24	Puncture Pb closer to seta P2 than P1	Puncture Pb closer to seta P2 than P1
25	Setae P1 and P2 equidistant to coronal suture	Seta P2 slightly farther from coronal suture than is seta P1
26	Setae P1 and P2 same length to P1 slightly longer	Setae P1 and P2 same length to P1 slightly longer
27	Puncture La much closer to seta L1 than A3, and less than 1/3 distance between L1 and A3	Puncture La much closer to seta L1 than A3, and less than 1/3 distance between L1 and A3
28	Alignment of puncture La and setae L1 and A3 somewhat aligned to forming a very obtuse triangle	Alignment of puncture La and setae L1 and A3 somewhat aligned to forming a very obtuse triangle
29	Seta O1 nearly in line with stemmata i and iv, equidistant to ii and iii; O1 slightly closer to iv than i.	Seta O1 nearly in line with stemmata i and iv, equidistant to ii and iii; O1 slightly closer to iv than i

APPENDIX 1. Continued

Character # of Motta	*M. confusa*	*M. curvifascia*
Head capsule (cont.)		
30	Angle formed between O2 and stemmata iv and v less than 90°	Angle formed between O2 and stemmata iv and v less than 90°
31	Seta O2 equidistant to stemmata iv and v	Seta O2 equidistant to stemmata iv and v
32,33	Seta O2 longer than O1 and O3, with O1 and O3 similar lengths	Seta O2 longer than O1 and O3, with O1 and O3 similar lengths
34	Seta O3 aligned with stemma v and "groove"	Seta O3 aligned with stemma v and "groove"
35	Puncture Oa ventral (toward antennal socket) to imaginary line between stemma i and seta A1	Puncture Oa ventral (toward antennal socket) to imaginary line between stemma i and seta A1
36	Puncture Ob aligned to stemma v and O3, and forming a triangle with stemma v and O2.	Puncture Ob aligned to stemma v and O3, and forming a triangle with stemma v and O2
37	Puncture Ob equidistant or nearer to stemma v relative to O2, and farthest from O3	Puncture Ob nearer to stemma v than O2 and farthest from O3
38	SO1 in ventral end of antennal socket so that distance of SO1 to end of antennal socket is less than 1/2 distance between SO1 and SO3	SO1 in ventral end of antennal socket so that distance of SO1 to end of antennal socket is less than 1/2 distance between SO1 and SO3
39	SO2 ventral to imaginary line connecting stemmata v and vi	SO2 ventral to imaginary line connecting stemmata v and vi
40	SO2 equidistant to slightly closer to stemma vi relative to stemma v	SO2 equidistant to slightly closer to stemma vi relative to stemma v
41	SO3 posterior to line between stemma vi and SO1	SO3 posterior to line between stemma vi and SO1
42	SOa between suture and imaginary line joining SO3 and G1, SOa same distance from suture as G1	SOa between suture and imaginary line joining SO3 and G1, SOa same distance from suture as G1
43	SOa falls on line between SO2 and nearest point of maxillary (ventral)suture, SOa is subtly closer to the suture than to SO3 and much closer to the suture than to SO2	SOa falls on line between SO2 and nearest point of maxillary ventral) suture, SOa is subtly closer to the suture than to SO3 and much closer to the suture than to SO2
44	SOb near antennal socket; distance of SOb to antennal socket about 1/2 that of SO3 to antennal socket	SOb near antennal socket; distance of SOb to antennal socket about 1/2 that of SO3 to antennal socket
45	SOb nearer, to slightly nearer, to SO3 than to stemma vi	SOb nearer, to slightly nearer, to SO3 than to stemma vi
46	G1 subtly closer to maxillary (ventral suture) relative to groove	G1 equidistant to groove and maxillary (ventral) suture
47	Ga aligned to line joining G1 and O3	Ga aligned to line joining G1 and O3
48	Ga nearer to O3	Ga nearer to O3
49	V1 nearer to "V" group than P2	V1 nearer to "V" group than P2
50	Stemmata all similar diameter	Stemmata all similar diameter
51	Similar distance between stemma i, ii, iii and iv	Similar distance between stemma i, ii, iii and iv
52	Stemma v closer to vi than to iv	Stemma v closer to vi than to iv
Labrum		
53	Seta M2 aligned or slightly basal to L1	Seta M2 aligned to L1
54	M2 aligned, to slightly dorsal, of line between M1 and L2	M2 basal to line between M1 and L2
55	M1 shifted slightly dorsal relative to M2	M1 aligned to slightly dorsal of M2
56	Distance between M1's greater than distance between M1 to M2	Distance between M1's greater than distance between M1 to M2
57	M2 longer than M1	M2 longer than M1
58	Puncture S located basal to M1 and M2	Puncture S located basal to M1 and M2
59	Puncture S equidistant to M1 and M2	Puncture S equidistant to M1 and M2 or a little closer to M2
60	Angle between the lines that connect M1 and M2, and M1 and the puncture S is 40° - 70°	Angle between the lines that connect M1 and M2, and M1 and the puncture S is 40° - 70°
61	Puncture equidistant to subtly nearer to M1 and M2 relative to posterior border	Puncture equidistant to M1 and M2 relative to posterior border
62	Puncture S basal to widest point of labrum	Puncture S basal to widest point of labrum
63	M3 on the distal border of the labrum	M3 on the distal border of the labrum
64	L2 nearer to L1 than L3	L2 nearer to L1 than L3
65	L1 level to widest point of labrum	L1 level to widest point of labrum
66	Less sclerotized region near the labrum notch and to M1 and M2	Less sclerotized region near the labrum notch and to M1 and M2
67	Less sclerotized basal patches absent	Less sclerotized basal patches absent
68	Internal border of the labral lobe smoothly curved	Internal border of the labral lobe smoothly curved
69	Basal angle of labrum notch obtuse	Basal angle of labrum notch obtuse

APPENDIX 1. Continued

Character # of Motta	*M. confusa*	*M. curvifascia*
Labrum (cont.)		
70	Ratio of notch length (= depth) to overall labral length (labral lobe to base) ~ 0.3; ratio of labral notch width, as measured between apices of lobes, to labral length ~ 1.1	Ratio of notch length (= depth) to overall labral length (labral lobe to base) ~ 0.4; ratio of labral notch width, as measured between apices of lobes, to labral length ~ 1.1
71	Ratio of labrum width (between L1's) to length (labral lobe to base) ~ 2	Ratio of labrum width (between L1's) to length (labral lobe to base) ~ 2
Mandible		
72	Fewer than three small molar teeth	Fewer than three small molar teeth
73	Incisors 2 and 3 similar lengths	Incisors 2 and 3 similar lengths
74	Lateral grooves radiating from each side of 4th incisor, one on outside more subtle than others, 4 grooves in total	Lateral grooves radiating from each side of 4th incisor, one on outside more subtle than others, 4 grooves in total
Body		
75	No tubercles present on the thorax	
77	Average seta length less than segment width	
78,79	Crochets arranged in a circle on segments A3-6, but A10 arranged in a semicircle; all crochet lengths similar	
80	Prolegs with more that 14 crochets on average	
81	Cervical sclerite absent on XD1 and XD2 and D1	
82	Seta D1 shorter than XD1 and XD2, XD1 and XD2 are equivalent in length	
83,87	Setae SD2 and SD1 aligned on T1, SD2 shifted posterior of SD1 on T2-A8, and SD2 shifted slightly posterior of SD1 on A9	
84	On segment T1 setae L1 and L2 slightly dorsal of spiracle with L2 between L1 and spiracle; on T2 and T3, L2 is at level of abdominal spiracles; on A1-A8 L1 and L2 below spiracle	
85,91	Setae D1 and D2 are equivalent lengths	
86	Seta SD2 closer to D2 than to SD1	
88	Seta SD2 ventral and posterior to D1 and D2	
89,94	Seta SD1 longer than L1 and equivalent to L2 on segment T1; on T2 & T3 setae SD1 and L2 equivalent and shorter than L1 and L3 (which are same length); SD1 equivalent to L1 and L2 on abdomen	
90	Seta L2 present on segments T1-A8	
92	Seta SD2 and D1 equivalent lengths and longer than D2	
93	SD2 shorter than SD1 on T1; SD2 longer than SD1 on T2 & T3; SD2 shorter than SD1 on abdomen	
95	L1 shorter than L2 on T1; L1 longer than L2 on T2 and T3 with L3 equivalent to L1; L1 and L2 equivalent on abdomen	
96	Additional SV seta on A2 only	
97	A9 with one less seta (L1 or L2) than A7 and A8	
98	Epiproct setae D1, D2, SD1 and L1 similar lengths	
99	P1 and SP1 setae present on A10	

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EXPERIMENTAL DESIGN AND THE OUTCOME OF PREFERENCE-PERFORMANCE ASSAYS, WITH EXAMPLES FROM *MITOURA* BUTTERFLIES (LYCAENIDAE)

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ABSTRACT. Investigations into adult host preference and the performance of larvae on different host plants have played a central role in ecological and evolutionary plant-insect research. Here I present two sets of experiments that address aspects of the experimental design of preference-performance assays, using a well-studied system of lycaenid butterflies. First, I compare results from sequential, no-choice oviposition assays to previous results reported from simultaneous choice tests with *Mitoura nelsoni*. Second, I describe an experiment in which the larvae of two closely related species (*M. nelsoni* and *Mitoura muiri*) were reared in parallel on plants in the laboratory and in the field to assess the potential influence of environmental conditions on performance. Results from the no-choice preference assays are consistent with previous results, suggesting that, at least in this system, the two types of experimental design lead to similar conclusions. The experiment rearing larvae in the field and in the laboratory revealed a significant effect of environment on pupal weights, but did not detect a species by environment interaction. Thus for pupal weights, a laboratory-based study is sufficient to compare performance between *M. nelsoni* and *M. muiri*. However, a species by environment interaction was observed for development time, which has implications for host-associated speciation in this group that would not have been detected in a solely laboratory-based study.

Additional key words: *Callophrys*, specialization, choice test, no-choice test.

Preference-performance assays are used to address a range of questions in the ecology and evolutionary biology of herbivorous insects (Dethier 1954; Thompson 1988; Jaenike 1990; Wackers 2007; Craig & Itami 2008). Preference refers to the choices made by ovipositing females or feeding individuals for different host plant species (Singer 2000), and performance refers to the development of juvenile stages on specific hosts. The questions addressed by preference-performance experiments may be as simple as: will a species of insect accept a particular species of plant as a host, and is the same plant a suitable host for larval development? Questions may also involve genetic variation and correlations among genetic elements: in particular, is preference for a particular plant species genetically correlated with the ability of larvae to utilize the same host species (Via 1986; Thompson 1988; Mayhew 1997). Experiments involving preference and performance are also central to the practice of biocontrol, in which behavioral and physiological host range must be determined before the release of a control agent (Marohasy 1998). These and related topics have been reviewed by many authors, including Jaenike (1990), Thompson & Pellmyr (1991), Craig & Itami (2008), and Berenbaum & Feeny (2008). The goal of this paper is to address two methodological and experimental issues involved in preference-performance assays: choice versus no-choice preference tests, and the influence of laboratory versus field conditions on performance experiments.

Two of the more common ways in which preference assays can be constructed include choice and no-choice tests (for a review of other experimental designs and related issues not discussed here, see Courtney *et al.* (1989), Singer & Lee (2000), Barton Browne & Withers (2002), Singer *et al.* (2002) Van Driesche & Murray (2004), and Mercader & Scriber (2007)). In choice tests, host plants are presented to an adult female or group of females in an array and the response is typically the number of eggs laid on the different plants in a set amount of time. In a no-choice assay, the behavioral response (oviposition) is scored with plants in isolation, often sequentially, with plants being presented one after the other to adults. Simultaneous choice tests have been criticized as being unrealistic, as different host plant species may not be in immediate physical proximity in the wild (Singer *et al.* 1992). On the other hand, an argument can be made that simultaneous choice tests are conservative: the juxtaposition of plants in an experimental arena could make it more difficult for an ovipositing female to make a choice (since information gathered from volatile plant cues may be overlapping or mixed).

In any event, the two types of test, choice and no-choice, potentially provide different and complementary information (Withers & Mansfield 2005). Consider a simple, hypothetical scenario: two host plants (A and B) are used by a particular insect herbivore. In choice tests, plant A is overwhelmingly preferred to the exclusion of plant B, but in no-choice tests both plants receive a comparable number of eggs from ovipositing females. It might be the case that the volatile and tactile cues that characterize plant A are sufficiently more stimulating to ovipositing females such that B is ignored in the presence of A. While in the absence of A, B is recognized as a suitable host and will

be utilized. The choice test tells us not only what could happen in the wild when plants are interdigitated or in very close proximity, but it tells us something about the inherent ranking of host cues by the herbivore (e.g. Thompson 1993). The no-choice test on the other hand might give a clearer picture of what could happen in the wild as a female moves from one isolated patch of plants to another. Choice tests are more common in the literature, perhaps because they are logistically more efficient. What is not often tested (and which I address here with one butterfly species) is how often the results from choice and no-choice tests provide different lines of information (as in the hypothetical example above), or how often results are congruent or redundant.

Preference experiments are often rather contrived in that females are typically presented plants under artificial conditions (cages or preference arenas), and in arrays or sequences that they might never encounter in the field (though more realistic preference tests have been conducted, e.g. Singer & Thomas 1988). In contrast to this, performance experiments need not be quite so highly abstracted from natural conditions: it is possible to rear larvae in the field by confining them to small cages or bags. Despite this, the majority of performance experiments have addressed the performance of larvae in laboratory conditions, often with larvae reared singly in petri dishes (Zalucki *et al.* 2002). Whatever measure of performance is taken (pupal weight, development time, etc.), it seems intuitively obvious that results may be biased by laboratory conditions. For example, the architecture of a given species of plant might provide a microclimate that allows larvae to feed throughout the heat of the day, resulting in faster development than on a host that does not have the same architecture (Alonso 1997). This effect would only be apparent if larvae were reared in the field. Other environment-dependent effects could include interactions with predators and parasitoids.

I used two species of lycaenid butterflies, *Mitoura nelsoni* Boisduval and *Mitoura muiri* H. Edwards, to address these issues in the design of preference and performance experiments. The oviposition behavior of *M. nelsoni* females in choice tests has been previously described: they have consistent preferences for their host incense cedar (*Calocedrus decurrens* Torrey), laying the most eggs on that host in both four-way and two-way choice tests involving other hosts of *Mitoura* in Northern California (Forister 2004, 2005a). Here I ask if the preferences of *M. nelsoni* females for incense cedar are expressed in no-choice tests as a willingness to lay eggs on incense cedar and a reticence to lay eggs on an alternate host when encountered in isolation. The larval performance of *M. nelsoni* and *M. muiri* on multiple hosts, as expressed in pupal weight and survival, has been previously described (Forister 2004, 2005a). Here I focus on one host, a host of *M. muiri*, and ask if differences between the two butterfly species in performance on that host are consistent between laboratory and field environments.

MATERIALS AND METHODS

Butterflies and plants. *M. nelsoni* and *M. muiri* are part of a complex of host-specific lycaenid butterflies in North America associated with plants in the family Cupressaceae which have been the focus of recent investigations into the ecology of speciation (Nice & Shapiro 2001; Forister 2004, 2005a, 2005b). *M. nelsoni* is found in association with incense cedar at low to middle elevations in mesic forests from southern British Columbia to Baja California. *M. muiri* is an edaphic-endemic associated with cypress hosts (primarily MacNab cypress, *Cupressus macnabiana* A. Murray, and Sargent cypress, *Cupressus sargentii* Jepson) on low elevation, ultramafic soils such as serpentine in California (Gervais & Shapiro 1999).

The experiments described here used *M. nelsoni* adults in preference experiments, and caterpillars of both species in performance experiments. The *M. nelsoni* adults consisted of wild-caught and laboratory-reared individuals. Wild-caught individuals were taken from the following locations in 2004 on the west slope of the Sierra Nevada Mountains near interstate 80: Drum Powerhouse Road and Lang Crossing (see Forister 2004 for more details on these locations). Laboratory-reared adults were part of a colony that was being maintained for other experiments at the University of California, Davis. These individuals were the offspring of females collected from a number of populations in the Sierra Nevada and North Coast Ranges in the previous season.

Larvae used in performance experiments were generated from individuals reared and mated in the laboratory. For both *M. nelsoni* and *M. muiri*, larvae were pooled from multiple lines without regard to genetic background within species. In other words, *M. nelson* larvae were the product of matings between *M. nelsoni* adults from a number of locations throughout California (and the same for *M. muiri*). These matings are described in detail in Forister (2005a).

Three host plant species were involved in these experiments: incense cedar (the host of *M. nelsoni*), Sargent cypress and MacNab cypress (hosts of *M. muiri*). For preference experiments, incense cedar and Sargent cypress were collected from Goat Mountain in the North Coast Range of California, where the two hosts grow sympatrically. For the performance experiments, MacNab cypress was used both in the field

and through collection from one location, Knoxville Public Lands, also in the North Coast Range.

Preference assays. In order to assess the oviposition behavior of *M. nelsoni* in no-choice assays, females were confined individually with sprigs of host plants in oviposition arenas (cylinders of wire mesh, 3600 cm^3). They were exposed to one host for 24 hours, and then switched to the other host for 24 hours (the two hosts, as mentioned above, were incense cedar and Sargent cypress). The switch from one host to the other was done in the early morning of the second day, before butterflies were active. Experiments were only conducted for 48-hour periods because previous experience with Mitoura butterflies had shown that females become considerably less vigorous and egg-laying begins to drop off after 48 hours when they are kept in a greenhouse in full sun (Forister, pers. obs.). At the start of the experiment, each female was haphazardly assigned to one of two groups, with one group being confined first with incense cedar, and the second group being confined first to Sargent cypress. Sugar water was applied to the cages as an artificial nectar source that was readily consumed by butterflies throughout the experiment. The number of eggs on plants was counted at the end of each interval as a measure of host preference (*Mitoura* butterflies very rarely ovisposit on any surface in preference arenas other than the host plants; and if eggs were found on the side of the cage they were not counted).

Results from preference assays were analyzed in two ways. First, the number of eggs laid by each female on the two hosts was treated as a pair in a nonparametric Wilcoxon matched-pairs test. This analysis addressed the question: which host received more eggs without reference to the order of the hosts? Second, a Wilcoxon rank-sum test was used to ask: does the first host encountered affect the number of eggs laid on incense cedar? In this case, each female is represented by one data point (the number of eggs laid on cedar), and females are identified as belonging to either the treatment that received incense cedar first or Sargent cypress first.

Performance assays. The goal of performance assays was to ask if differences in performance between the two butterfly species observed in the laboratory (Forister 2004, 2005a) are also observed in the field. To address this question, ten trees of MacNab cypress, the host of *M. muiri*, were selected at a field site that has been studied previously (Knoxville, see Forister 2004). Trees were selected haphazardly within a small area (approximately 100 square meters), and caterpillars of both *M. muiri* and *M. nelsoni* were reared to pupation simultaneously on these trees in the field and on cuttings from these trees brought back to the laboratory. Caterpillars in the laboratory were reared in groups of five in large drinking cups nested within smaller cups so that the cut ends of branches could be pushed through holes in the larger cup and into water held in the smaller cup. Upon pupation, pupae were weighed on a Mettler Toledo microbalance to the nearest hundredth of a milligram. Caterpillars that became part of the field component were reared initially in the laboratory through the first instar. They were then transferred to the field, where they were reared to pupation in groups of five in spun mesh bags enclosing tree branches. Each of the ten trees in the field had two bags (one *M. muiri* bag and one *M. nelsoni* bag). Caterpillars in bags were checked weekly and moved to new branches on the same trees when foliage had been depleted. Upon pupation, pupae were removed from bags, brought back to the laboratory and weighed. In addition to pupal weight, survival and days to pupation were recorded for both the laboratory and field-reared individuals.

Analyses of variance (ANOVA) using restricted maximum likelihood (REML) mixed models were used to analyze results from performance experiments (Littell *et al.* 1996). Fixed factors in models included species, location (field or laboratory), and an interaction between species and location. Random factors were tree, and interactions between tree and species, and between tree and location. Rearing group is not included in models because values within groups (for pupal weight, development time and survival) were simply averaged prior to analysis (individuals within groups are not statistically independent).

No transformations were found to be necessary to meet the assumptions of ANOVA for pupal weight or development time. Residual error from analysis of survival (the fraction of individuals surviving to pupation within each rearing group) was highly non-normal (even following arcsine transformation) due to the large number of groups in which survival was 100%. Therefore, two separate nonparametric Wilcoxon rank-sum tests were performed to compare survival between the two species in the laboratory and in the field. JMP-IN software, version 7.0 (SAS Institute, Cary, NC, U.S.A.), and Kaleidagraph, version 3.6 (Synergy Software, Reading, PA, U.S.A.), were used for nonparametric analyses (both for survival data and preference results, described above), and PROC MIXED in SAS, version 9.1 (SAS Institute, Cary, NC, U.S.A.), was used for REML analyses of variance.

Results

Preference assays. A total of 45 *M. nelsoni* females were tested in no-choice assays using incense cedar, the

host of *M. nelsoni*, and Sargent cypress, the host of *M. muiri*. As can be seen in Fig. 1a, females laid a majority of their eggs on incense cedar in these no-choice assays ($T = 4.63$, $P < 0.0001$). The behavior of females was not influenced by the order in which plants were presented to them: a comparable number of eggs was laid on incense cedar regardless of whether that host was presented first or second in sequence (Fig 1b; $T_1 = -1.11$, $P = 0.26$).

Performance assays. A total of 185 larvae were reared to pupation in 39 rearing groups (20 in the laboratory and 19 in the field; larvae from one *M. muiri* group in the field escaped). As has been observed in previous work (Forister 2004), *M. nelsoni* individuals develop to pupal weights that are greater than *M. muiri* (on average 10% greater), even though the host in question is the natal host of *M. muiri*. The results reported here demonstrate that this difference (between the two species) is not affected by rearing environment (Fig 2a, and note the insignificant species by location interaction in Table 1). In contrast, rearing environment did have a differential effect on the development time of the two species: in the field, *M. muiri* individuals reach pupation 4.62 days earlier than *M. nelsoni* individuals (Fig. 2b, Table 2). In general, larvae of both species developed more slowly in the field, and this might be because they did not feed at night: when checking the bags in the early morning, I found larvae to be inactive, while larvae in the laboratory are capable of feeding throughout the night. There were no significant differences between the

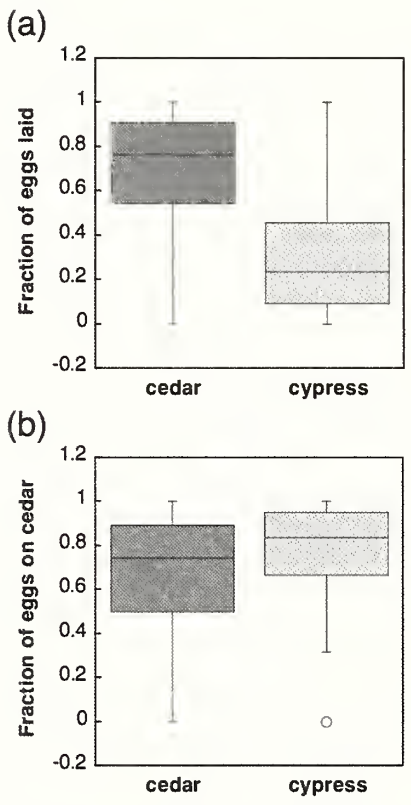

FIG. 1. Results from preference assays illustrated as box plots. The same data is shown in two different ways in (a) and (b): data shown in (a) is the fraction of eggs laid on the two hosts, while (b) shows the influence of experimental sequence in sequential no-choice assays on oviposition behavior. In other words, in (b), the data shown is the fraction of eggs laid on incense cedar for females which were exposed to that plant first (the left box), and for females which were exposed to cypress first (the right box).

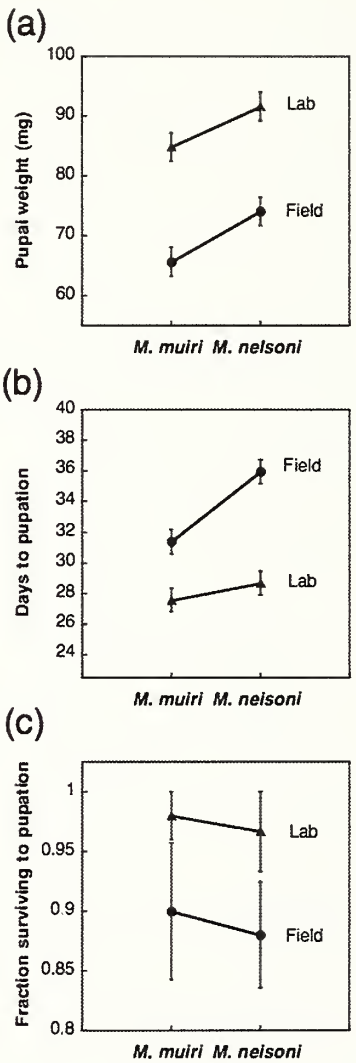

FIG. 2. Means and standard errors from assays of performance in the laboratory and in the field. Statistical results for pupal weight (a) and days to pupation (b) are shown in Tables 1 and 2 respectively. See text for more details related to survival (c).

survival of *M. nelsoni* and *M. muiri* caterpillars in the laboratory ($T_1 = 0$, $P = 1.0$) or in the field ($T_1 = 0.51$, and $P = 0.61$) (Fig. 2c).

Differences among individual trees had a significant effect on pupal weight (Table 1), but not on development time (Table 2). Although tree had an effect on pupal weight, this was not influenced by rearing environment, nor was there a significant species by tree interaction. In other words, larvae of both species did better on certain trees, and this was true whether larvae were reared in the field or on cuttings from the same trees in the laboratory. In order to better visualize the influence of individual trees on pupal weight, Fig. 3 shows the correlation between weights of larvae reared in the field and in the laboratory. One outlier has been excluded from the relationship shown in Fig. 3: one *M. nelsoni* rearing group had high mean pupal weight in the field (80.03 mg), but unusually low weight in the laboratory (66.9 mg). With the outlier excluded, the correlation is significant: Pearson product-moment correlation of 0.73, $P = 0.0006$; with the outlier included the correlation is 0.37, $P = 0.12$.

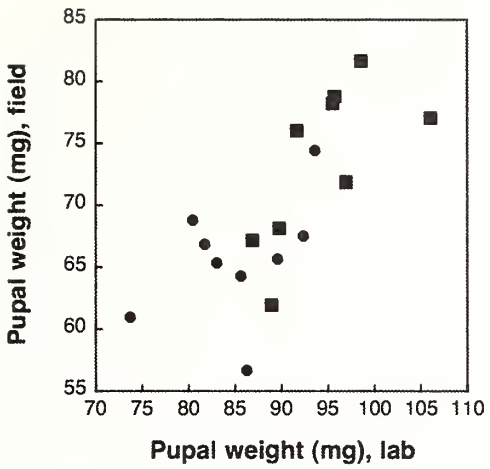

FIG. 3. Comparison of pupal weights in the field versus pupal weights in the laboratory. Each point corresponds to a group of larvae reared on foliage from a single plant in the field and in the laboratory. Each host plant is shown twice, once as the host of *M. muiri* larvae and once as the host of *M. nelsoni* larvae (circles are *M. muiri*, squares are *M. nelsoni*). A single outlier was excluded, see text for details.

DISCUSSION

M. nelsoni females express a clear preference for their natal host, incense cedar, in both choice tests (Forister 2004, 2005a), and no-choice tests, as reported here (Fig. 1). Choice tests are more efficient from the point of view of experimenter effort: there is less manipulation in choice tests, as plants do not need to be changed part way through the test (as compared to a no-choice design with sequential replacement of hosts). The results reported here suggest that, at least in the *Mitoura* system, choice tests provide equivalent information to no-choice tests. There are two important caveats to this conclusion. First, these results should not be used to infer that the two types of choice test are equivalent in other systems. Rather, the results reported here highlight the utility of exploring both types of assay, and the possibility that in some systems choice tests may be sufficient. Second, while it is true that choice and no-choice assays with *M. nelsoni* lead to similar conclusions about the relative ranking of the two hosts by ovipositing females, there may be situations in which no-choice tests would still be uniquely useful. For example, no-choice tests could be used to survey for variation among

TABLE 1. Results from analysis of pupal weights. Degrees of freedom and *F* ratios are reported for fixed effects, covariance estimates and standard errors for random effects. Significant *P* values are shown in bold text.

Source	NDF	DDF	*F*	*P*
Species	1	26.3	16.8	**0.00040**
Location	1	26.3	97.3	**< 0.0001**
Species x location	1	26.3	0.21	0.65
		Covariance	SE	*P*
Tree		19.0	13.1	**0.0095**
Tree x species		0	-	-
Tree x location		0	-	-

TABLE 2. Results from analysis of development time (days to pupation). Degrees of freedom and *F* ratios are reported for fixed effects, covariance estimates and standard errors for random effects. Significant *P* values are shown in bold text.

Source	NDF	DDF	*F*	*P*
Species	1	13.3	13.2	**0.00300**
Location	1	26.3	97.3	**< 0.0001**
Species x location	1	26.3	0.21	0.24
		Covariance	SE	*P*
Tree		0.354	0.93	0.33
Tree x species		0.945	1.36	0.24
Tree x location		0.836	1.34	0.26

females in preference for a less preferred host, while such variation could potentially be harder to detect in choice tests where females always spend a majority of their time ovipositing on the preferred host. No-choice tests could also be used to study factors (such as egg load) which may influence "motivation" and lead to the acceptance of an otherwise less-preferred host (Singer *et al.* 1992).

With the performance results reported here, it is apparent that a comparison between the two species for at least one element of larval performance (pupal weight) is not greatly influenced by rearing environment. *M. nelsoni* pupae are bigger than *M. muiri* pupae, and individuals reared in the laboratory are bigger than individuals reared in the field (Fig. 2a), but being reared in the laboratory or the field does not change the relative sizes of *M. nelsoni* and *M. muiri* pupae. The foliage quality of individual trees was also consistent across rearing environments (Fig. 3). The vast majority of performance experiments are done in the laboratory (Zalucki *et al.* 2002), thus the results reported here are heartening: not only may laboratory performance (as measured by pupal weight) be an accurate reflection of performance in the field (at least in the absence of natural enemies), but intraspecific variation in plant quality may in some cases also be reasonably studied under laboratory conditions. Osier *et al.* (2000) reported a similar consistency between performance in the laboratory and in the field on particular plant genotypes using gypsy moth larvae and quaking aspen clones.

The performance results reported here are also interesting in the light of a scenario of host-associated speciation that has been described in *Mitoura*. Differences in host preference are believed to be a key mechanism in the diversification of this group (Nice & Shapiro 2001; Forister 2004, 2005a), as has been suggested for a number of other phytophagous insect systems in which adults mate and oviposit on their host plants (Berlocher & Feder 2002; Drès & Mallet 2002). Divergent host preferences are expected to evolve in association with host-specific larval adaptations, particularly when divergence is in sympatry or parapatry (Fry 2003) (which appears to be the case for *Mitoura*). *M. nelsoni* fits this model nicely: females have strong preferences and larvae attain considerably larger pupal weights on incense cedar (larger than *M. nelsoni* larvae reared on other hosts of *Mitoura* in northern California, and larger than other *Mitoura* larvae reared on incense cedar). In contrast, *M. muiri* females have strong host preferences but *M. muiri* larvae do not attain greater pupal weights or have higher survival on their natal cypresses relative to *M. nelsoni* larvae on the same hosts. The present study suggests a previously undetected component of local adaptation in *M. muiri*: faster development than *M. nelsoni* on MacNab cypress in the field. Why this difference would only be manifest in the field is not known, though one possibility is that *M. muiri* larvae may be able to feed over a slightly wider range of temperatures than *M. nelsoni* larvae. Faster growth may reduce exposure to natural enemies (Williams 1999), or extreme climatic events (Fordyce & Shapiro 2003). In particular, faster development at low elevations in the dry, inner North Coast Range of California might allow larvae to pupate before temperatures become unfavorably high (three days before the end of the experiment, a maximum daily temperature of 40 degrees Celsius was recorded at the field site). Although the adaptive significance of faster development in the field is unknown, this is a difference between *M. nelsoni* and *M. muiri* that would not have been observed in a solely laboratory-based study.

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NOCTUA COMES IN ONTARIO: AN INTRODUCED CUTWORM (NOCTUIDAE: NOCTUINAE) NEW TO EASTERN NORTH AMERICA

Additional key words: grape, tobacco, Palaearctic.

The Lesser Yellow Underwing, *Noctua comes* Hübner, [1813], is an Old World cutworm moth that was introduced in North America in the Vancouver, British Columbia, area around 1982 (Neil 1984; Copley & Cannings 2005). It has since spread eastward in British Columbia as far as the Okanagan Valley, and south into Washington and central Oregon, and continues to expand, but has not yet crossed the Continental Divide (Lafontaine 1998, J. Donald Lafontaine pers. com.). The slow expansion of *Noctua comes* in the Pacific Northwest in the last twenty-five years is in stark contrast to the spread of its highly invasive congener, the Large Yellow Underwing, *Noctua pronuba* (L.), which was introduced in Halifax, Nova Scotia, around 1979 and in the same time period has traversed the continent (Neil 1981, Powell 2002), quickly becoming abundant in most areas.

On 15 August 2006 I collected a fresh male *Noctua comes* (Fig. 1) at a mercury vapor light in my garden in urban Toronto, Ontario, Canada (43.674°N, 79.337°W). On 25 September 2006 a second worn male was collected at the same location. The specimens are deposited in the Canadian National Collection (CNC), Ottawa, and the identification was confirmed by J. Donald Lafontaine. This is the first report of *Noctua comes* in eastern North America. In 2007, two additional specimens (both female) were collected at the same location on 24 September and 26 September (specimens in collection of the author). Despite regular moth collecting in downtown Toronto for a number of years, yielding over 150 species of noctuid moths, *Noctua comes* has not previously been detected. Its sudden appearance suggests that it has only recently become established here and, over 3000 km east of its known North American range, undoubtedly represents a separate introduction from the Palaearctic or a secondary introduction from the Pacific Northwest. With the increasing number of recent introductions of Old World noctuids in the Northeast (Mikkola & Lafontaine 1994, J. Donald Lafontaine pers. com.), and the proximity to the Great Lakes–St. Lawrence Seaway (and the port of Toronto a few kilometers away), a European origin seems more likely. Dual introductions on the Atlantic and Pacific coasts, often almost simultaneously, have been noted with some frequency in the Lepidoptera (Ferguson 1996, Mikkola & Lafontaine 1994, Miller 1999, Powell & Passoa 1991).

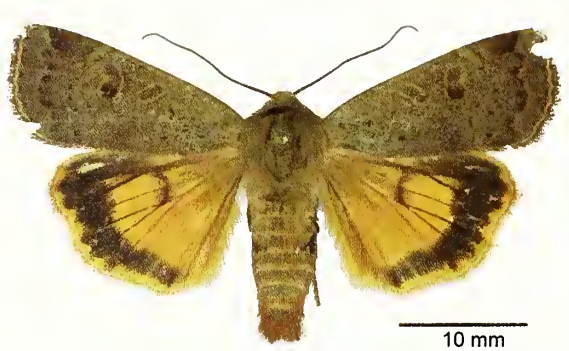

Fig. 1. *Noctua comes*, male, Toronto, Ontario, Canada, 15 August 2006.

Larvae of *Noctua comes* feed at night on a wide variety of herbaceous plants in open areas including weedy species, cultivated plants, and grasses (Poaceae) and in spring also climb to feed on low woody plants (Lafontaine 1998, Waring *et al.* 2003). It is a minor pest of grape (*Vitis* L.) (Vitaceae) and tobacco (*Nicotiana* L.) (Solanaceae) in the western Palaearctic, and larvae were recently found feeding on developing grape buds in vineyards in Washington (Sannino & Espinosa 1999, James 2007).

Additional records from Toronto are expected and the species should be watched for in southern Ontario, southwestern Quebec and the Great Lakes states. *Noctua comes* can be distinguished from *Noctua pronuba* by its smaller size (forewing length = 16 to 21 mm) and by the presence of a conspicuous black discal spot on the hindwing. The living moth with wings closed may suggest a species of *Abagrotis* Smith more than a small *pronuba*. Diagnostic characters of the genitalia and larvae of *Noctua comes* and *N. pronuba* are provided by Lafontaine (1998). Additional Palaearctic species of *Noctua* are illustrated in Fibiger (1993, 1997). The early stages of *Noctua comes* are described and illustrated by Sannino & Espinosa (1999). It has a single brood annually and overwinters as a larva; the flight season extends from July to September, with extreme dates in June and October in the Pacific Northwest and the British Isles. Specimens from British Columbia in

the CNC from February and March are labeled "from nursery" and were likely reared from larvae found in greenhouses.

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ERYNNIS FUNERALIS OVIPOSITS ON EXOTIC *ROBINIA PSEUDOACACIA* IN WESTERN ARGENTINA

Additional key words: Fabaceae

Butterflies are adapting to exotic host plants worldwide, including high elevations in the Andes (Shapiro 2006) and in the South American subantarctic (Shapiro 1997). This note reports the apparently widespread use of the naturalized North American tree Black Locust (*Robinia pseudoacacia* L. (Fabaceae)) as an oviposition substrate and presumptive host plant of a presumably native skipper in western Argentina.

In late afternoon on 24 January 2008 at Chos Malal, Neuquen Province, I watched a female *Erynnis funeralis* (Scudder & Burgess) lay three eggs in succession on coppice growth of *R. pseudoacacia* in town. Alerted to this behavior, I then observed another female in a different part of town lay one egg on this plant three hours later. I subsequently saw repeated instances of oviposition, always on growth less than 4m tall and often in shade, at Las Lajas, Neuquen; in the city of Mendoza, Mendoza Province; and around Calingasta and Barreal, San Juan Province, all over the next three weeks, for a total of >30 ovipositions by at least 8 different females. Though the species was common, I never observed oviposition on other substrates.

Pastrana (2004) includes this plant as a host based on Aravena (1983), adding that that record might be based on reared material provided by J. Williamson from the Province of LaPampa. Scott (1986) lists this as a host of *E. zarucco* (Lucas), at that time considered conspecific, in the United States. He also lists *Robinia neomexicana* A. Gray as a host of *E. funeralis*. Although alfalfa (*Medicago sativa* L., Fabaceae) is the most widely-cited host of *E. funeralis* in both the United States and Argentina, and is regularly visited as a nectar source, I have never seen any trace of oviposition or preoviposition behavior directed toward it in 30 years' experience in Argentina.

Black Locust is widely naturalized, having escaped from urban cultivation in Argentina, and is routinely found as a participant in synthetic woody riparian communities recruited from the horticultural flora in irrigated zones in the arid and semiarid west. *Erynnis funeralis* is a consistent inhabitant of these communities as well as appearing in urban gardens and parks; its distribution in western Argentina is broadly concordant with that of *Robinia pseudoacacia*. A significant element of the western regional fauna is similarly restricted to

irrigated zones in association with naturalized weedy hosts (Shapiro, unpublished data). It is not known if this butterfly is native to the region or is itself naturalized; it is the only member of its genus in the Southern Cone of South America.

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COMMENTS ON LARVAL SHELTER CONSTRUCTION AND NATURAL HISTORY OF *URBANUS PROTEUS* LINN., 1758 (HESPERIIDAE: PYRGINAE) IN SOUTHERN FLORIDA.

Additional key words. Egg stacking, hostplant, oviposition, clutch size.

The Bean Leaf Roller (*Urbanus proteus* Linn.) is a common and widespread skipper (Hesperiidae) found from southern United States south to Argentina (Smith *et al.* 1994). Early observations on its natural history (Scudder 1889) have been supplemented with details from various parts of its range (Greene 1970, 1971a; Kendall 1965; Moss 1949; Riley 1975; Skinner 1911; Smith *et al.* 1994; Young 1985), particularly in Florida (Quaintance 1898), where it is a pest on leguminaceous crops (Green 1971b; Quaintance 1898; Watson & Tissot 1942) and where there exist documented seasonal movements (Urquhart & Urquhart 1976). Like most skippers (Greeney & Jones 2003), the larvae of *U. proteus* construct and live in shelters made from the leaves of the food plant, but only two authors have described or pictured these shelters in any detail (Quaintance 1898; Young 1985). In fact, detailed knowledge of larval shelter construction for most skippers is weak or nonexistent for all but one widely distributed North American species, *Epargyreus clarus* Cramer, 1775 (Jones *et al.* 2002; Lind *et al.* 2001;Weiss *et al.* 2003). As shelters may prove useful in resolving phylogenies (Greeney & Jones 2003), here we present our observations of shelters from a population of *U. proteus* in southern Florida.

We made observations at Burns Lake Campground (25°53'N, 81°13'W) in Big Cypress National Preserve, Collier County, Florida. On 30 December 2005, at 14:15, we observed a female *U. proteus* ovipositing on the under surface of a leaflet of *Vigna luteola* (Jacq.) Bentham (Leguminaceae). She laid three dull yellow eggs in an evenly spaced row, and then flew out of sight. This observation prompted us to search foliage of other *V. luteola* plants, and resulted in the discovery of 26 additional clutches of hatched and unhatched eggs.

At hatching, larvae consume only the top portion of the eggs (pers. obs.), and we were able to use the remaining egg fragments to determine clutch size from all 27 clutches (mean = 2, SD = 1.1, range = 1–5). Most clutches were located on the under surface of mature leaves (n = 24), but occasionally on leaf petioles (n = 3). Within a clutch, eggs were placed adjacent to (touching) or up to 1 mm from other eggs. One exception was a clutch of three eggs found stacked end to end such that only the bottom egg was attached to the leaf surface (Fig. 1). Similarly, Quaintance (1898) reported a clutch size of 1–6 and noted that eggs were frequently laid in a stacked fashion, 3–4 eggs high. Young (1985), however, recorded only single egg clutches in Costa Rica.

In addition to the eggs, we found a total of 50 larvae representing the following instars: 36 first, 8 second, 3 third, 2 fourth, and 1 fifth. We removed larvae from their shelters and carefully determined their ages using the prior experience of HFG with the larvae of related species. We also watched as 3 first-instars constructed new shelters after removal from their original shelters. By examining shelter construction and comparing our observations to previously constructed shelters, we determined that larvae build 3–5 shelters as they develop, and that these belong to three shelter types. First through third instars were found inside shelters built by excising a small triangular portion of the leaf margin and creasing it into a tent-shaped lid (Greeney & Jones 2003; group III, type 10, two-cut stemmed

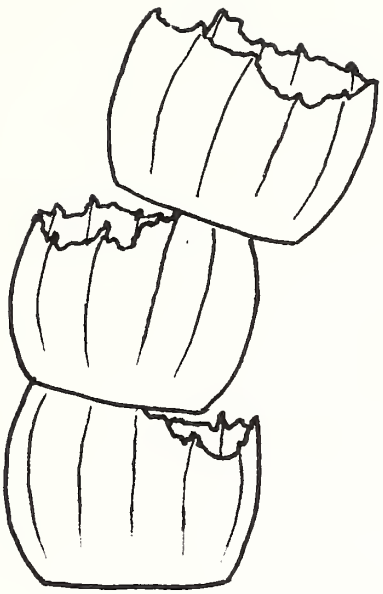

FIG. 1. Three *Urbanus proteus* egg shells found on the under side of a leaf, Burns Lake Campground, Collier County, Florida, December 2005.

shelters). These *U. proteus* shelters were, in fact, very similar to shelters described for *E. clarus* (Weiss *et al.* 2003), and would be considered the same type under the classification of Greeney & Jones (2003). Like *E. clarus*, the shelter cuts of *U. proteus* were always oriented in a distinct fashion in relation to the leaf base; the longest cut always being distal. The most obvious and consistent difference we found was the lack of a "notch" in the cut closest to the leaf petiole in shelters built by *U. proteus* larvae (Fig. 2). Early instar shelters were still "tented" into a distinct peak, however, by pinching together (using multiple silk ties) a small section along the margin of the shelter lid. The result was a shelter similar in appearance to that built by *E. clarus*, but arrived at by slightly different means (ie. without the notch). Fourth instars were found, one each, inside a shelter created by silking two leaves together (group I, type 4, two-leaf shelter) and one formed by silking several leaves together (group I, type 3, multi-leaf shelter). We found the single fifth instar feeding adjacent to several leaves silked together (group I, type 3 shelter) at around 17:45.

Our observations bring to light several important aspects of egg laying and larval shelter building. Firstly, species building superficially similar shelters may use slightly different cut patterns or construction techniques to arrive at the finished product. Therefore, shelters will prove useful in testing phylogenetic hypotheses (Greeney & Jones 2003) only if we examine shelters and their construction in much more detail than previously reported (but see Greeney & Warren 2003, 2004; Lind *et al.* 2001; Weiss *et al.* 2003).

Secondly, our observations, and observations of late instars of other pyrgines (HFG unpublished) and coeliadines (Common & Waterhouse 1972), suggest that there may be little difference between the "type 3" and "type 4" shelters distinguished by Greeney & Jones (2003); these shelter types being defined by the number of leaves included in the shelter. In later larval stadia, *U. proteus* silks together two or more leaves or leaflets into a silk-lined pocket (this study, Quaintance 1898). Young (1985), however, observed only two leaves used in late instar shelter construction. We conclude, therefore, that the number and arrangement of the various leaf parts used is likely related to the relative size and shape of the host plant leaves rather than to any innate shelter building behavior. In other words, larvae simply spin silk, pulling leaves (or parts thereof) around themselves until they are sufficiently covered. Similarly, *E. clarus* shows variation in the number of leaves used in late instar shelters, varying with size of the host plant leaf (M. Weiss pers. comm.). Based on these observations , we suggest that "type 3" and "type 4" shelters, as defined by Greeney & Jones (2003), should be merged into one "multi-leaf" shelter type, regardless of whether the shelter includes two or more leaves or leaflets.

Finally, the three egg shells we found stacked end to end showed a different emergence pattern than described in previous observations of lepidopteran oviposition. Several species of the nymphalid genus *Hamadryas* Hübner are also known to deposit eggs one on top of another, sometimes in chains of more than 10 eggs (Muyshondt & Muyshondt 1975b, 1975c). To

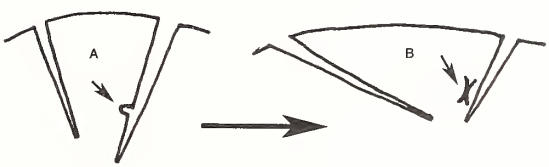

FIG. 2. Comparison of cut patterns for first instar shelters of (a) *Epargyreus clarus* (redrawn from Weiss et al. 2003) and (b) *Urbanus proteus*. Large arrow points towards the base of the foodplant leaf to show orientation of shelters. Small arrows point to (a) position of notch made by *E. clarus* to aid in tenting the shelter and (b) position of silk laid down to pinch shelter into a tented peak by *U. proteus*.

emerge from the eggs, *Hamadryas* larvae create an opening in the side of the egg. Previous discussions on patterns of egg laying and larval emergence in nymphalids suggest an evolutionary signifigance to the correlation between side emergence and egg stacking: side emergence being necessary to avoid damaging eggs laid above (Muyshondt & Muyshondt 1975a). Our observation of egg stacking in *U. protens* showed emergence from the top, suggesting that emergence from the side of the egg is not a necessary adaptive response to eggs laid in stacks. While we were unable to clearly illustrate top-emergence in Figure 2, our direct observations show that this was indeed the case. Figure 2 also shows that the eggs of *U. protens* were not laid directly centered above the egg below, as illustrated in Muyshondt & Muyshondt (1975b, 1975c) for *Hamadryas*. It is possible that this means of attaching stacked eggs represents an alternative adaptation allowing eggs to be laid in stacks.

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IAN FRANCIS BELL COMMON (23 JUNE 1917 TO 3 JUNE 2006)

Ian Francis Bell Common (23 June 1917 to 3 June 2006) was an outstanding Australian entomologist who exerted a major influence on studies of Lepidoptera, not only in Australia but throughout the World.

I first met Ian in 1968 when he was researching his book *Butterflies of Australia* and commenced work with him at Commonwealth Scientific and Industrial Research Organisation (CSIRO), Division of Entomology, Canberra, in November 1970. We worked on many moth groups in the Australian National Insect Collection (ANIC) and our close working association continued through Ian's retirement until his death.

He was brought up in Toowoomba, Queensland, and after a spell in his father's business he entered Toowoomba Grammar School and matriculated in 1937. He attended the University of Queensland graduating with a B.A. (first class honors in Philosophy) in 1941 and B. Agr. Sc. in 1945 (with honors in 1947). In 1941 he volunteered for military service but was rejected because of his feet.

In 1944 Ian was appointed Research Officer with the Queensland Department of Agriculture and Stock and was employed part time by CSIR Division of Economic Entomology to work under Ken Key to study clothes moths infestations in Brisbane wool stores. A letter to Ian survives from this time written by A.J. Turner, then doyen of Australian amateur lepidopterists, outlining the different clothes moths (Tineidae) known from Australia. Ian continued at the University of Queensland graduating with a M.A. in Philosophy in 1946 and M. Agr. Sci. in 1953. He was later, in 1969, awarded a D. Agr. Sci. by the University of Queensland. From December 1944 to June 1945 Ian worked for the Queensland Department of Agriculture and Stock at Biloela and then at Rockhampton from 1945 to 1948. He worked principally on cotton pests, tomato pests and the yellow-winged locust.

His interest in Lepidoptera had developed early and he had tales of collecting with school friends around Toowoomba and there are many specimens dating from his early collecting now in the ANIC. For many years there was a small cabinet, made by Ian from silky oak wood, housing immaculate, minute, reared Gracillariidae collected in his youth but now all incorporated into the main collection. In his formative years and the early years of his career Ian worked without close contact with other lepidopterists. Few people could have developed the skills and knowledge that Ian possessed without close contact with experienced, practising lepidopterists. That he overcame this immense challenge so successfully is a measure of the man. Although this close contact with other lepidopterists was denied to him he greatly admired F.A. Perkins then lecturer in entomology at the University of Queensland.

While at university Ian met Jill Dowzer who had come to Brisbane from Rockhampton to study Arts. They met again when Ian was posted to Rockhampton and married in 1946. They had two daughters Frances and Jennifer. Throughout his subsequent life Ian was to benefit greatly from the constant support of his wife and family.

Ian was appointed to CSIR Division of Economic Entomology on 25 May 1948 after a State-

Commonwealth tussle eventually involving Prime Ministerial intervention. He became Technical Secretary to A.J. Nicholson, Chief of the Division, and able to work half time on the taxonomy of Lepidoptera. In 1947 the Turner collection had been transferred to the Division of Economic Entomology which was an added incentive for Ian to join the Division. In 1951 he transferred to full-time work on cereal crop and pasture caterpillars.

Ian's early years with the Division were marked by a series of world-class revisions of pest moth groups in Australia including *Heliothis, Agrotis, Persectania, Pectinophora, Scirpophaga* and *Epiphyas*. Also at this time he published his classic work on the bogong moth migration. In the 1960s he started revisionary work on the Australian tortricine Tortricidae following his work on *Epiphyas* and *Merophyas*. He later worked extensively on the higher classification of the Lepidoptera culminating in the internationally widely acclaimed Lepidoptera chapter in *Insects of Australia* (1970 and revised with E.S. Nielsen in 1991). In this phase of his work he described one new superfamily (Immoidea), two new families (Carthaeidae and Lophocoronidae), one new subfamily (Munychryiinae) and a new tribe (Epitymbiini). Following this he commenced work on the Oecophoridae, the favorite subject of his long and abiding interest in the vast Australian fauna. Throughout his career he also published on relevant or interesting items as they arose.

Altogether he published about 100 papers and seven books on Lepidoptera. The first books were the Jacaranda guides *Australian Moths* (1963, revised 1966) and *Australian Butterflies* (1964). In 1972 *Butterflies of Australia* (with D.F. Waterhouse) was published with a revised edition in 1981. This book revolutionized butterfly studies in Australia empowering a growing band of butterfly enthusiasts to make many original discoveries and observations. In retirement he published the massive and internationally significant *Moths of Australia* (1990), which was awarded the Whitley Medal by the Royal Zoological Society of New South Wales and his three great volumes on the *Genera of Australian Oecophorinae* (1994, 1997, 2000).

Besides his huge published contribution, Ian built the ANIC Lepidoptera collection from Turner's small, but important and well-identified, collection into the immense resource it is today. Ian's exquisitely preserved, set and labelled specimens of microlepidoptera still dominate the ANIC collection. He recognized the need to maintain a good working collection and, whatever the backlog of accessions, always kept a well-sorted, named, core so that the ANIC could maintain an identification capacity across the whole Order. The good order, high curatorial standards and large holdings of the collection attracted many top overseas Lepidopterists to Australia and greatly facilitated their work on the Australian fauna. With Ken Key, Ian helped in establishing protocols for the high quality maintenance and operation of the collection well in advance of their time.

To build a collection of a little-known and neglected fauna Ian recognized the need for field work and in the 1960s he and Murray Upton embarked on a series of renowned trips to various parts of Australia. They employed extensively the MV light for the first time and the expeditions were highly efficient camping trips dedicated to collecting with not a minute wasted. They were planned to the last can of beans and nothing was allowed to go wrong. These trips opened the eyes of many to how little was actually known of the fauna. Ian and Murray experimented with many light and sheet combinations and designed very efficient light traps which effectively separated out beetles and other rugged insects from the fragile moths permitting for the first time trapped moths to be obtained in good condition in a warm country where insect activity is intense. Ian introduced the extensive study of moth genitalia to Australia and helped develop new staining techniques and a protocol for the successful mounting of moth wings for detailed study of the venation.

He participated in a 1953 expedition with C.B. Williams of Rothamstead, England, to the Pyrenees to observe insect migration followed by an academic year at the University of Cambridge and four weeks at the British Museum (Natural History) to study types. In 1966 he spent an additional six months at the BM(NH) photographing types of Australian microlepidoptera and dissecting the types of numerous Australian Oecophoridae. In 1979 he visited many overseas colleagues and collections and also gave the presidential address at the Lepidopterists' Society meeting in Fairbanks, Alaska.

Through his career Ian attracted dedicated colleagues who helped each other and obtained by synergy more than each could have attained individually. The Lepidoptera unit settled into a three person team, Ian as scientist, an experimental officer (Ted Edwards) and an assistant (most notably Vanna Rangsi), which achieved an efficiency now no longer possible when scientists have to grovel for funding and assistants are seen as short-term and dispensable. On Ian's retirement this synergy was maintained by his successor Ebbe Nielsen, who encouraged and facilitated some of the most productive projects of Ian's life. This was continued by Marianne Horak following Ebbe's

untimely death. Ian had been one of Marianne's mentors who, with John Dugdale, encouraged her on an entomological career specializing in Tortricidae. Ian always maintained close collaborations with people who used his identifications and advice, overseas colleagues, the State museums, agriculture departments and amateur lepidopterists. He was a wonderful lepidopterist; as 'at home' in telling stories of moths and collecting with amateur lepidopterists as he was with discussing the higher classification with distinguished overseas colleagues. He was a master in all branches of the subject.

Ian achieved the rank of Chief Research Scientist in July 1974 and retired to Toowoomba in June 1982 when he became an Honorary Fellow of the Division of Entomology and in 2003 became an Emeritus Fellow. In retirement he continued to collect for the ANIC and his later books and papers were retirement projects strongly supported by CSIRO Entomology and the Australian Biological Resources Study. Throughout his career Ian remained a dedicated scientist and had no aspirations to enter administration.

He was a member of the Entomological Society of Queensland from 1938 and Secretary 1939-40 and a foundation member of the Australian Entomological Society in 1965 becoming Vice-President in 1969-72, President in 1980-81 and an Honorary Life Member in 1987. He was a member of the Lepidopterists' Society from 1949 and was Vice-President 1957, 1st Vice-President 1965, President in 1978-79 and became an Honorary Life Member in 1987. He was a foundation member of the Ecological Society of Australia, a member of the Linnean Society of New South Wales from 1956 and a Fellow of the Royal Entomological Society from 1966. He was also an honorary member of the Sociedad Hispano-Luso-Americano de Lepidopterologia from 1982.

Ian's work was most widely recognized through the award of the Karl Jordan Medal by the Lepidopterists' Society in 1996 for his contributions to the study of Lepidoptera and he became an Officer of the Order of Australia in 2001 for his outstanding contributions to entomology, science and education in the community. He received the Jacob Hübner Award for Lepidoptera Systematics from the Association for Tropical Lepidoptera in 2003.

Ian was a wonderful person to work with. He saw the implications and ramifications of taxonomic work (and much else) very clearly and often well beyond the view of many contemporaries. He was scholarly, dedicated, thorough, meticulous (a word he employed) as well as very hard-working. Few minutes were wasted. He took great pains to excel in all he did. Yet with this he was indulgent of neophytes provided they had application, interest and enthusiasm. He was courteous, quietly spoken and modest. He was approachable, open handed with his immense knowledge and respectful of other views. He greatly valued the critical faculty which could separate the sound from the unsound. He could also express himself concisely and cuttingly when he found foolishness.

Jill Common has kindly made information on Ian's early years available. A manuscript, an article in *The Canberra Times* on 29 January 2000 and an article in *Qantas* in January 2001 all by Brad Collis have been helpful. Biographies in *The Lepidopterists' Society-Commemorative Volume (1945-1973)*, in *Biologue No. 24* by Ted Edwards and in Murray Upton's *A Rich and Diverse Fauna* have been of great assistance. A useful manuscript source was the nomination for the award of the Order of Australia prepared by the late Ebbe Nielsen. A manuscript biographical note by Ian himself was most valuable. Further biographical sources can be found in Murray Upton's book. Other original sources are housed in the ANIC Archives. A complete list of Ian's publications may be found in Greg Daniels' *Bibliography of Australian Entomology 1687-2000.*

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LOS LEPIDOPTEROS ARGENTINOS: SUS PLANTAS HOSPEDADORAS Y OTROS SUSTRATOS ALIMENTICIOS. By Jose A. Pastrana. 334 pp. ISBN 987-21319-0-2. $40 US to purchasers in Mercosur countries; $70 to SEA members, otherwise $80 US elsewhere. South American Biological Control Laboratory USDA-ARS and Sociedad Entomologica Argentina, Buenos Aires (from whose Web site it may be purchased). Publication date: 2004.

My favorite professor in graduate school was the late William L. ("Bill") Brown, Jr., who had a gift for telling it like it was. He frequently admonished his students to beware of what he called "validation by frequency of citation", the process whereby errors become institutionalized by mere repetition. It is a process that is nowhere more common or more deleterious than in the listing of host plants for phytophagous insects. Back in 1983 I published a note in a Mexican journal, identifying several such errors which had crept into the Mexican literature from ours. The worst offenders in this regard are omnium-gatherum compilations, which rarely exercise discretion in evaluating the included material and all too frequently do not trace the source. Sometimes one compilation will incorporate all the dubious material from previous ones, compounding the problem.

In 1972 Arthur Allyn arranged for the posthumous publication of Harrison M. Tietz's card file of life-history information on North American Lepidoptera, which he had been accumulating during his decades as a faculty member at Pennsylvania State University. By the time it appeared it was 20 years out-of-date, but still valuable. Because it was well-referenced if uncritical, it at least allowed one to trace a variety of howlers that had crept into widespread usage—including some of the ones I figured in my 1983 Mexican article. I still use my well-thumbed and -annotated copy, but often wish someone would publish a detailed critical addenda and corrigenda. I am not holding my breath, and the science has moved on.

Now history has repeated itself in Argentina. Like Tietz, the late Jose Pastrana accumulated a bibliographic file over several decades, but died (at age 87) before it could be prepped for publication. The task of organizing it, standardizing the format and modernizing the taxonomy was shared by several colleagues: Karen Braun, Guillermo Logarzo, Hugo Cordo and Osvaldo DiIorio. They consulted a variety of specialists, including John Brown, Adriana Chalup, Don Davis, Fernando Navarro, Patricia Gentili, Gerardo Lamas (who reviewed the butterflies), Alma Solis and Maria Elvira Villagran. But the task clearly overwhelmed them, and the result is very much less than satisfactory. Here is DiIorio speaking (my very rough translation):

> "When the Catalog of Phytophagous Insects of Argentina was being prepared, we found the unpublished manuscript of Pastrana…How to determine which records pertained to Argentina? The manuscript mentioned the host plants of each species of Lepidoptera without any indication of localities or bibliographic references to the sources….For a certain number of plants the original source was never determined, though one could detect a certain pattern of repetition of data by Pastrana himself….In future editions or addenda we can add the missing information and corroborate the corresponding plant-insect associations."

In other words, all the usual problems are present here, and more so than in Tietz. And as will become plain, even when sources are documented, they are often inaccessible, so that a real critical evaluation is not possible.

Undoubtedly some taxonomic groups are in better shape than others. Since I work on the Argentine Pierini and have published more life-history and biological information on this fauna than anyone else (virtually none of which is cited by Pastrana! — though my work overlapped his active years), and this group is better-known than most, I have chosen to illustrate the nature and magnitude of the problems by working through the couple of pages devoted to my own little group. My evaluations are based on my own 30 years of work in Argentina, and to save space I will not cite the various pertinent Shapiro publications. What is important is how reliable the data in Pastrana are. If what follows is at all representative…

p.201: The only given host plants of *Hypsochila wagenknechti wagenknechti* (Ureta) are "Asteraceas: *Aplopappus bailahuen*; *Senecio* sp.." The bug is a Crucifer-feeder, and this hoary error is based on old records of nectar sources, ultimately going back to Ureta himself (?).

p.203: *Tatochila autodice autodice* (Huebner): In addition to legitimate hosts (glucosinolate plants, i.e. Brassicaceae and Tropaeolaceae) many other, dubious records are cited: "Fabaceas (*Medicago sativa*) (Berg,1895,Anonymous 1930, Lizer and Trelles 1941) (Hayward 1969, ex Joergensen, Biezanko 1959, Viana and Williner 1974); Solanaceas: *Cestrum elegans* (Biezanko 1959), *C. nocturnum* (Biezanko 1959), *C. parqui* (Giacomelli 1915, ex Burmeister 1878),(Lizer

and Trelles 1941, Biezanko 1959, Hayward 1969, Viana and Williner 1974); *C. corymbosum* (Berg 1875, Giacomelli 1915, Hayward 1969).

Tatochila autodice blanchardii Butler: Lists only Tropaeolaceae, omitting the perfeetly valid records on Brassicaceous hosts.

Tatochila mercedis mercedis (Eschholtz): Oddly, the text lists the distributional records from the Province of Neuquen as "doubtful," when hardly anything in this book is similarly qualified. But the records are aceurate!

Phulia nymphula (Blanchard): "Tropaeolaceae: *Tropaeolum polyphyllum* (Reed, Hayward 1969 ex Reed)." A glueosinolate specialist but apparently eonfined to plants in rosette growth form, making this exuberant herb highly unlikely.

p.204: *Tatochila orthodice* (Weymer) is recorded from "Brassicaceas": *Brassica* sp.; *Cheiranthes* (sic) *annus* (sie)(Hayward 1969), *Lobularia maritima* (Hayward 1969); Tropaeolaceas: *Tropaeolum* sp. (Hayward 1969). Despite the high degree of specificity, all of these records are wrong. The true host plant of this speeies remains undetermined but is almost certainly Fabaceous; it is not a feeder on glucosinolate-containing plants. And *Cheirantlius* are ehemieally odd, and normally avoided by Pierines.

Tatochila stigmadice (Staudinger): again listed on "Brassieaceas (Hayward 1969)", again incorrectly.

Tatochila theodice theodice (Boisduval) is listed on Tropaeolaceae, attributed to Giacomelli (1915). It is strietly a legume feeder.

Theochila maenacte maenacte (Boisuval) is claimed to be a Brassieaceous feeder (Biezanko, Ruffinelli and Carbonell 1957; Hayward 1969, from them). It isn't. Again, its true host remains unknown but is suspeeted to be Fabaceous.

Most of these errors show clear trains of repetition, eventually converging to Hayward (who in his later years committed many errors, some of which I have documented elsewhere) and thence to Pastrana. There is a clear tendency to assume that "if it's a White, it eats Crueifers." In South America this does not work. The attribution of Brassicaceous hosts to Legume feeders is actually repeated in the entry for *Colias vauthieri* (Guerin), which lists "Brassicaceas (Havrylenko 1949)!" (It also lists alfalfa, which this speeies does not eat, attributing the reeord to Crouzel and Salavin 1969.) The very persistent records of *Tatochila autodice* on the Solanaceous plant *Cestrum* are a special problem that needs to be dealt with definitively one way or the other. The chemistry is so outrageously different that the association must be viewed as highly unlikely at best.

This volume is valuable for its huge bibliography of often very obscure references, most of which, alas!, are unobtainable via interlibrary loan services within the United States (I've tried). (The most obscure ones cited below are just as cited by Pastrana, if you feel inclined to push the envelope of your favorite retrieval system.) If you can't get them, you can just go ahead and cite them like everybody else, and keep the old errors in cireulation to continue to confound those of us trying to study the interaction of coevolution and phylogeny! I consider it a sign of Divine intervention that Braby and Trueman (2006) did not consult this porqueria when they compared host relationships to molecularly-inferred Pierid phylogeny. May others with similar objectives do the same!

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PAPILLONAGES: UNE HISTOIRE CULTURELLE DU PAPILLON. By Nicolas Witkowski. 143 pages, copiously illustrated; 10.5" x 11.75". ISBN 978-2-02-089821-8; EUR 40.00. Seuil, Paris. Publication date: 4 October 2007.

This is, to my knowledge, only the second attempt at a coffee-table "cultural history" of butterflies. I reviewed the other (Manos-Jones,2000) in the *News* (Shapiro, 2001). Its author was a mere autodidact-amateur. Nicolas Witkowski, however, is a French Intellectual and as such his book demands a more formal review. Witkowski is a professor of physics, a cultural historian, a popularizer of science and a translator of Stephen Jay Gould. His forte is drawing connections between scientific themes and cultural trends, a very French Intellectual thing to do. In this visually stunning book he displays his virtuosity. To quote from the jacket blurb (all the translations that follow are my own):

> Symbol of beauty and lightness, but also emblem of the soul and of metamorphosis, the butterfly has always fluttered between triviality and seriousness, fickleness and profundity, debauchery and metaphysics. Every epoch has conferred its own particular "take" on this ambivalence. Our own has placed the butterfly somewhere between chaos theory and a snarky tattoo....the butterfly has always adapted itself to the feel of the times and offers a faithful mirror of our most secret anxiety...

The book is divided into nine chapters, each accompanied by sidebars and digressions and a wonderful array of color (often full-page) illustrations. Because of Witkowski's cross-cutting style, only very rough descriptions of the chapters are possible:

I: *The invention of the butterfly.* Very early representations of the butterfly in art, from cave paintings through the Middle Ages and across cultures and continents. Inaddition to an illuminated manuscript (by Jean Bourdichon, the most distinguished of the French artists who incorporated Lepidoptera in such work—butterflies are much commoner in books produced in Ghent and Bruges, but this is after all a French product!), this chapter reproduces a very rare Yuan Chinese scroll (circa early 14th Century) with an anatomically-correct swallowtail. Almost all butterflies in East Asian art are highly stylized; this is an extraordinary exception.

II: *The ephemeral and the immortal.* Butterflies in European Renaissance art, from the "busy" bouquets of the Dutch still-life masters to idealistic and romantic works of the Masters. (Includes a two-page spread of a bilateral gynandromorph of *Cymothoe sangaris* and a discussion of its sexual resonances.)

III. *The woman chrysalid.* Focuses on the life and work of Maria Sibylla Merian, reproducing several of her exuberant plates and contrasting their dynamism with the usual static portrayal of insects in isolation. Also discusses Albert Seba and reproduces a painting by Jan van Kessel in which mounted butterflies and other insects are being displayed.

IV. *A butterfly.* A study of the butterfly-and-moth-haunted dreamscapes of the artist Henry Fuseli.

V. *Cunning hunts.* An examination of butterfly collecting as it developed beginning in the 17th Century, particularly in the tropics, and how it fed into the Darwinian revolution. Includes a reproduction of a tropical swallowtail from Alexander Marshall's famous manuscript (1660) in the Philadelphia Academy of Natural Sciences.

VI. *The moral of the butterfly.* Female entertainers at the turn of the century dressed as butterflies; cartoons and illustrations of fables and nursery rhymes; Jean-Henri Fabre as raconteur of true-life butterfly fables; Dante Gabriel Rossetti as romanticizer. The strangest thing in this chapter is a macabre painting by Felicien Rops, a fantasy melding butterfly, woman, and death.

VII. *Nabokov's blues.* Familiar territory thanks to recent books by others. Includes some of V.N.'s fanciful butterfly sketches (juxtaposed with contemporary butterfly tattoos), and the Meadow Brown with the bird's head from Hieronymus Bosch, featured in a Life magazine article about Nabokov in 1947.

VIII. *The wings of chance.* A riff on Edward Lorenz's butterfly metaphor in chaos theory, now almost universally known but seldom understood.

IX. *Under the sign of the butterfly.* A summing-up. The tone is best conveyed by a fairly extended quote which, however, still falls within the boundaries of "fair use:"

> At the end of this personal voyage transformed into a cultural history, I rediscover in the Western approach to the butterfly the old drama of which Goethe was the harbinger: *What can one learn of Nature by analysis?* What more can one get besides a cadaver impaled on a blue steel pin? What remains of the magic of flight under the frozen gaze of the researcher? The quarrel is as old as modern science—more or less four centuries—but today it takes on a new sense: the era of great butterfly massacres is at hand [referring to the crisis of biodiversity—A.M.S.]....What science is worth what one sacrifices...the art of seeing, of loving that which one sees? The beauty of the butterfly, immediate, presenting itself to passive contemplation, is irremediably destroyed by

> any effort at analysis. How can one be fully satisfied by such fleeting joy? How can one resist the temptation to capture…and to crush between one's fingers the object of one's love? There are the important questions that underlie our everlasting interest in the wonderful butterfly, the precious "little soul" that always causes us such pain because we cannot catch it.

If you are not used to the flowery, intricate idiom of French intellectual discourse this passage may turn you off. Even if you are used to it, it may do so. Whether or not you take all the pretentiousness seriously (and you are permitted, as a mere Anglo-Saxon, to dismiss it as airy twaddle), this is a magnificent book and highly recommended for your coffee table, whether or not you read French. I say this even though it omits any reference to my favorite cultural touchstone for the butterfly in French—the nursery rhyme that goes *"Faites pipi sur le gazon/pour embeter les papillons."* (Make weewee on the grass, it drives the butterflies nuts.)

The last image in the book is very disquieting and in the tradition of Medieval *Memento mori*. It is a two-page photograph, larger than life, of a box of Dermestidized 19th-Century *Morpho* specimens – glorious pieces of blue wings and meticulously handwritten labels adrift in a sea of beetle frass. Make of it what you will.

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